BENTHIC-PELAGIC COUPLING ON THE ANTARCTIC CONTINENTAL SHELF: IMPACTS OF SEASONAL PHYTODETRITUS DEPOSITION ON THE BENTHIC COMMUNITY

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ABSTRACT

The West Antarctic Peninsula (WAP) shelf experiences highly seasonal fluxes of particulate organic carbon following the retreat of winter sea-ice, resulting in deposition of labile food for benthic detritivores (i.e., "benthic-pelagic coupling"). A time-series study (Nov 99 - Mar 01) was conducted to determine timing and magnitude of bloom deposition to the WAP shelf, and consequences for benthic ecology. Impacts on microbial biomass, persistence of labile organic material in sediments, and effects of pulsed food inputs on benthos are discussed. Despite substantial temporal changes in particle flux, labile compounds (chloropigments, bioavailable amino acids) in near-surface sediments varied modestly, with evidence of elevated flux limited to the top 3 cm. Despite high sediment inventories of labile organic matter and microbial biomass, organic matter remineralization balanced sinking particle flux, and rates were comparable to temperate shelves. High substrate concentrations required for microbial mineralization of organic matter at low temperatures may promote the existence of a "food bank" of labile material for benthic detritivores in WAP shelf sediments. Stable isotopes in benthos and potential food sources were used to examine sources and sinks of particulate organic material reaching the sediments, and to establish trophic linkages among the most abundant benthic megafauna. The broad (>14‰) range in $\delta^{13}C$ values of surface plankton was narrowed considerably in sediments, where little seasonal or interannual variability in isotopic signature was observed. Bloom-derived detritus appears to be the primary source of organic material supplied to benthic detritivores; however, seasonal variability in the supply of this material is not mirrored in the sediments, and only to a minor degree in the benthic fauna. This pattern suggests substantial inertia in benthic-pelagic coupling, whereby the sediment ecosystem integrates long-term variability in water column productivity. The dominant pattern of recruitment observed was one of essentially continuous recruitment, with localized peaks (in space and time) observed in some taxa. This pattern is consistent with the presence of a "food bank" for detritivores, such that recruitment is not limited by the presence of a seasonally available food source. Post-settlement controls may also be important influences determining localized recruitment peaks in particular seasons or locations.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1. INTRODUCTION

Growing concern over global climate change has stimulated widespread interest in the sequestration of organic carbon in marine sediments. The fate of particulate organic carbon (POC) deposited at the sea floor must be known if the dynamics of this long-term carbon reservoir are to be quantified. Efforts to quantify the flux and fate of surface-derived organic particles have recently evolved into investigations of the many linkages between water-column and benthic processes, termed "bentho-pelagic coupling" (e.g., Graf, 1992). Already widely recognized in continental-shelf ecosystems, bentho-pelagic coupling via periodic phytodetritus deposition events has now been reported for numerous deep-sea sites (e.g., Billett *et al.*, 1983; Lampitt, 1985; Smith *et al.*, 1996; Fabiano *et al.*, 2001; Beaulieu, 2002). Understanding these benthic-pelagic linkages in various regions of the world's oceans may yield important insights into climate driven changes in both benthic and pelagic ecosystems.

In areas where coupling can be especially tight, such as the relatively shallow waters on continental shelves, organic particle fluxes constitute a key food source for major components of benthic food webs, including suspension feeders, deposit feeders, and sediment microbes. Thus, in many regions, pelagic ecosystem dynamics significantly influence material cycles and benthic ecological processes in sediments (e.g., Gooday and Turley, 1990; Graf, 1992; Ambrose and Renaud, 1995; Piepenburg *et al.*, 1997; Pfannkuche *et al.*, 1999; Duineveld *et al.*, 2000). Due to bentho-pelagic coupling, a "footprint" of surface-derived primary production often appears in benthic community dynamics and sediment chemistry on the underlying shelf. However, recent data suggests sediments may dampen the effects of temporal or spatial variability in primary production patterns in the water column (Nedwell *et al.*, 1993; Mincks *et al.*, 2005). Thus, depending on the timing and magnitude of the response by various benthic components to phytodetritus deposition events, sediment communities may provide integrated views, in space and time, of ecosystem dynamics in the waters above (e.g., Piepenburg *et al.*, 2001; Hannides and Smith, 2003; Smith *et al.*, 2005).

Bentho-pelagic coupling on the Antarctic continental shelf

Because of extreme seasonal variability in production cycles, polar regions have recently received significant attention in bentho-pelagic coupling research (e.g., Grebmeier *et al.*, 1988; Grebmeier and McRoy, 1989; Grebmeier, 1993; Ambrose and Renaud, 1995; Grebmeier and Cooper, 1995; Piepenburg *et al.*, 1997; Renaud, 1998; Grant *et al.*, 2002; Baldwin and Smith Jr., 2003; Smith *et al.*, 2005). High latitude oceans are subject to intense seasonal variations in sunlight, sea-ice cover, and water-column stratification, which produce extraordinary seasonality in pelagic primary production, accompanied by rapid settling of bloom detritus to the seafloor. In the near-shore Antarctic shelf environment, particle flux is orders of magnitude larger during spring and summer sea-ice retreat than in ice-covered winter months (Wefer *et al.*, 1988; Dunbar *et al.*, 1989; Honjo, 1990; Dunbar *et al.*, 1998). This intense seasonal production/deposition pattern over such a vast continental shelf (roughly 11% of global shelf area; Clarke and Johnston, 2003) makes Antarctic waters particularly intriguing targets for bentho-pelagic coupling studies. Further, if a significant amount of detritus rapidly deposited in summer months is respired slowly beneath winter ice cover, the CO_2 produced may be trapped beneath the ice and advected into deeper water before it can be released to the atmosphere (Yager *et al.*, 1995).

The rapid sinking of particulate organic carbon (POC) produced during the high-latitude summer bloom appears to allow large proportions of pelagic production to reach the seabed with relatively minimal water-column processing (Honjo, 1990; Karl *et al.*, 1996; Nelson *et al.*, 1996; Fileman *et al.*, 1998), suggesting tight bentho-pelagic coupling. These rapid sinking rates result from a number of factors, including high summer-bloom abundance of large diatoms, which tend to sink quickly out of the water column (DiTullio *et al.*, 2000). Sea-ice algae, released into surface waters during summer ice-edge retreat, also facilitate efficient transport of primary production to the seafloor. Polysaccharides secreted by these algae enhance aggregate formation—and thus rapid particle sinking—upon release from sea-ice (Riebesell, 1991; Hong *et al.*, 1997). In addition, pelagic food webs in Antarctic shelf waters can be relatively short, with krill feeding on diatom blooms and producing large, fast-sinking fecal pellets (Wefer *et al.*, 1988; Bathmann *et al.*, 1991; Smith *et al.*, 2005).

Despite this evidence suggesting potentially tight coupling between water-column and benthic processes, several characteristics of the Antarctic shelf may actually weaken potential benthic-pelagic linkages relative to other shelf systems. For example, ice loading on the Antarctic continent results in an unusually deep (500-1000 m) continental shelf (Eisma, 1988; Clarke and Johnston, 2003) characterized by complex topography and ocean circulation (Hofmann and Klinck, 1998; Smith *et al.*, 1999). Resultant increases in particle sinking time and water-column recycling of surface production may weaken translation of the water-column productivity signal to the shelf floor (Smith *et* *al.*, 2005). In addition, low bottom-water temperatures may slow benthic respiration of organic matter relative to temperate shelf sediments (Pomeroy and Deibel, 1986; Pomeroy *et al.*, 1991). These unique aspects of the soft-sediment Antarctic shelf environment may affect the strength of bentho-pelagic coupling, relative to shallower, hard-substrate habitats around Antarctica, and to shelf systems elsewhere in the world.

Effects of seasonal organic inputs on Antarctic benthos

Seasonal phytodetritus pulses to the deep sea constitute a major food source for benthos in an otherwise food-poor environment, and can dictate seasonal responses in benthic processes such as growth and reproduction in the absence of any other seasonal cues (e.g., temperature, light availability) (e.g., Tyler *et al.*, 1982; Tyler, 1988; Tyler and Young, 1992). Since Antarctic waters are similarly food-poor throughout much of the year, and also lack seasonal changes in other environmental cues such as temperature, similar impacts of phytodetritus deposition on benthic ecology have historically been expected (e.g., Clarke, 1988; 1992). Many such processes have only recently begun to be explored (reviewed in Smith *et al.*, 2005; see especially Barnes *et al.*, 1996; Stanwell-Smith and Barnes, 1997; Stanwell-Smith *et al.*, 1998; Galley, 2003; Suhr *et al.*, 2003), but the seasonality of food supply to the benthos does appear to be a major structuring force in at least some taxa.

Microbial response to phytodetritus deposition

Bacterioplankton biomass in surface waters of the Antarctic Peninsula region has been shown to increase by as much as six-fold from winter to summer months, although abundance of *Archaea* increases substantially during winter months (Karl *et al.*, 1996; Murray *et al.*, 1998; Church *et al.*, 2003). However, phytoplankton production exhibits even greater winter minima, such that bacterial production in the water column can exceed that of phytoplankton in winter and early spring (e.g., Rivkin, 1991). Bacterioplankton may thus be a crucial source of food for protozoan and some metazoan grazers during periods of low phytoplankton productivity.

Bacterial response to the summer bloom pulse in Antarctic continental shelf *sediments* has been little studied. The nature of the benthic microbial response to the short (4 - 8 wk) summer bloom is difficult to predict based on existing bacterial biomass and sediment community oxygen consumption (SCOC) data. Short generation times (hours to days) generally allow bacteria to respond quickly to pulsed nutrient inputs, as has been widely observed in sediments following episodic inputs of phytodetritus (Graf, 1989; Gooday and Turley, 1990; Lochte, 1992). Observed correlations in deep-sea sediments between microbial biomass and metabolism, and organic carbon rain rates (Meyer-Reil and Koster, 1992; Smith *et al.*, 1997), suggest that bacterial abundance should increase in Antarctic sediments during post-bloom periods of POC deposition. However, extremely low Antarctic bottom-water temperatures (-2.0 – 1.0°C) may slow microbial remineralization of phytodetritus deposited on the seafloor (Pomeroy and Deibel, 1986; Pomeroy *et al.*, 1991). On the other hand, if temperature effects on bacterial growth are mediated by substrate availability, as has been observed in other areas, then bacteria might be released from growth limitation following the spring bloom (Pomeroy *et al.*, 1991; Wiebe *et al.*, 1992; Wiebe *et al.*, 1993; Rutter and Nedwell, 1994; Nedwell, 1999; Yager and Deming, 1999). Thus, while low temperature alone may not ultimately limit microbial metabolism in Antarctic species, it may combine with low substrate concentrations to limit microbial activity throughout much of the year (i.e., during low-productivity months or years).

Seasonal patterns of SCOC on the Antarctic shelf point to weak seasonality in microbial respiration relative to the pelagic production regime. In shallow waters around Signy Island, particulate flux varied ~80-fold from summer to winter, whereas sediment community oxygen consumption varied only 5-fold or less (Nedwell *et al.*, 1993). In addition, SCOC appears only weakly coupled to organic-matter flux in various Antarctic shelf locations, exhibiting much stronger inter-annual than seasonal variability (Nedwell *et al.*, 1993; Baldwin and Smith Jr., 2003; C. Smith and DeMaster, in prep.). Thus, based on SCOC rates, microbial activity on the Antarctic shelf appears much less seasonally variable than primary production in the water column. This pattern suggests that other factors (such as very low temperatures) may be limiting microbial processes in these Antarctic sediments.

Metazoan response to phytodetritus deposition

The extreme summer/winter contrast in pelagic production has long been thought to leave Antarctic benthos extremely resource limited during the winter months (e.g., Clarke, 1988), such that food availability would be the dominant control, particularly on feeding behavior and reproduction, in Antarctic invertebrates. Suspension feeders were once thought to experience long periods of starvation, with cessation of feeding beneath winter sea ice (Clarke, 1988; Barnes and Clarke, 1995). However, some species are now known to cease feeding for only a few months in midwinter, if at all (Barnes and Clarke, 1995; Orejas *et al.*, 2003). Additional work suggests Antarctic taxa may utilize multiple suspension feeding strategies, with some species adapted to feed seasonally on the large summer-bloom phytoplankton and rapidly accumulate biomass and energy reserves during summer months, while others feed continuously at low rates on smaller microplankton and resuspended sediment particles throughout much of the winter (Orejas *et al.*, 2000).

Studies evaluating seasonality of deposit feeding in Antarctic taxa have yielded equivocal results. The sea urchin *Sterechinus neumayeri* was reported to cease egestion of sediments, and show no evidence of feeding, for 4 to 5 months during winter (Brockington *et al.*, 2001; Brockington and Peck, 2001). Metabolic rates and body-tissue mass in *S. neumayeri* declined during the non-feeding period, indicating that the winter was a time of starvation. In contrast, a number of other deposit-feeding echinoderms showed little or no evidence of winter cessation of feeding, or of declining energy reserves in body tissues (Galley, 2003). Further, these and other deposit feeders from the same location contained recently deposited sediment in their guts during all seasons sampled, evidenced by year-round presence in guts of excess ^{234}Th activity (McClintic, 2002), a commonly used tracer of freshly deposited organic material in sediments (e.g., Lauerman *et al.*, 1997; Stephens *et al.*, 1997; Miller *et al.*, 2000). ^{14}C measurements of gut sediments also supported observations that deposit-feeders were consuming relatively young, labile organic carbon throughout the year (Purinton, 2005).

Given the relationship between food availability and both parental investment in, and survival of offspring, temporal variability in either pelagic or benthic food resources can substantially impact spawning, gametogenesis, and recruitment patterns (e.g., Tyler *et al.*, 1982; Tyler, 1988; Clarke, 1992). Timing of seasonal bloom-derived flux events could be a selective pressure on planktonic larvae or recruiting benthic juveniles if particulate food, either in the water column or sedimented to the seafloor, is a limiting resource. Alternatively, flux events could influence adults by providing necessary nutrient stores for gamete production, or merely serving as a synchronization mechanism for spawning events (Tyler, 1988; Eckelbarger and Watling, 1995).

To date, patterns of reproduction and life history for Antarctic macro- and megabenthos have been widely debated, with relatively few supporting data. Much of the discussion and the existing data focus on the echinoderms and gastropods (e.g., Bosch and Pearse, 1990; Pearse, 1994; Clarke, 1996; Poulin and Feral, 1996; Galley, 2003). In these groups, evidence of a direct correlation between spawning and organic nutrient flux is still somewhat equivocal (Pearse *et al.*, 1991; Clarke, 1992; Tyler *et al.*, 1994; Ambrose and Renaud, 1997). While some Antarctic species spawn during the summer bloom (Pearse and Giese, 1966; Bosch *et al.*, 1987; McClintock and Pearse, 1987; Pearse *et al.*, 1991; Gutt *et al.*, 1992; Peck and Robinson, 1994; Meidlinger *et al.*, 1998) many others do not (Gutt *et al.*, 1992; Shreeve and Peck, 1995; Stanwell-Smith and Clarke, 1998). Thus, larvae of benthic invertebrates can be found in the water column year-round, with many species of planktonic feeding larvae in the water column even during winter periods of low food availability (e.g., Stanwell-Smith *et al.*, 1998). Low temperature-effects on metabolic rates may allow larvae to survive for extended periods (months to years) without necessarily relying on particulate food resources (Shilling and Manahan, 1994). For example, in the Antarctic sea urchin *Sterechinus neumayeri*, early development appears to occur at a similar rate whether or not particulate food is available in the water column (Marsh and Manahan, 1997; Marsh *et al.*, 1999). In addition, alternative nutritional sources, such as DOM or bacteria, may be exploited (Rivkin *et al.*, 1986; Manahan, 1990; Pearse *et al.*, 1991; Peck, 1993; Shilling and Bosch, 1994). Whatever the mechanisms involved, this pattern of year-round larval production suggests that the reproduction of Antarctic benthos is not necessarily tightly coupled to the summer phytoplankton bloom.

If larval production is, at most, weakly coupled to bloom dynamics, recruitment to the benthos should show equally little seasonality. Recruitment studies for Antarctic shelf benthos are quite scarce, but available data do suggest weak coupling to summer blooms. Settling plate studies in shallow waters essentially showed continuous recruitment at low rates throughout the year, with superimposed seasonal patterns in some instances (Bowden *et al.*, in review; Stanwell-Smith and Barnes, 1997). McClintock *et al.*, (1988) also suggest continuous recruitment for the Antarctic asteroid *Odontaster validus*. Timing of recruitment events has not yet been studied on the deeper, soft-sediment regions of the Antarctic shelf. If sediments do indeed dampen temporal variability seen in the overlying waters, then similarly weak seasonal patterns would be likely in these areas as well.

Research Objectives

My dissertation research was conducted within the framework of a collaborative project designed to evaluate the impact and fate of the summer phytodetritus pulse on benthos of the West Antarctic Peninsula shelf. This project, called FOODBANCS (FOOD for Benthos on the ANtarctic Continental Shelf), involved a 16-month field program sampling the deep (600 m) Antarctic Peninsula shelf. FOODBANCS program participants collectively tested the hypothesis that phytodetritus deposited seasonally on the Antarctic continental shelf would be mixed rapidly into sediments, and degraded slowly due to low bottom-water temperatures, such that bloom-derived material would accumulate in sediments, forming a persistent "food bank" for benthic detritivores.

The primary goal of my research was to contribute to the assessment of the effects of summer bloom-derived sedimentation events on the benthic community. Specifically, I sought to determine the degree of seasonality in the supply of organic material available to the benthos, and to examine the impact of this seasonality on various aspects of benthic ecology, including microbial biomass, food-web structure and feeding strategies, and recruitment of macro- and megafauna. This research, and its relevance to the broader FOODBANCS objectives, is detailed in the chapters that follow.

In **Chapter 2**, the degree of seasonality in food availability experienced by benthos is compared to magnitude and timing of summer bloom-derived flux events recorded in sediment traps. Seasonal changes in the size of the sediment organic pool available to detritivores (i.e., the sediment "food bank") were determined using several standard measures of organic content. In addition, degradation rates of various organic pools were modelled using advection-diffusion equations. The results indicate that seasonal primary productivity patterns detected in sediment traps are dampened in sediments, such that soft-sediment benthic communities do not experience the same degree of seasonality in food availability as pelagic organisms. Further, microbial biomass response to the summer phytodetritus pulse was surprisingly small. A temperature-substrate limitation hypothesis is put forth to explain reports of seemingly high sediment microbial respiration rates with apparently slow degradation and remineralization of organic material.

Seasonal changes in sources and sinks of organic material reaching the shelf benthos, as well as trophic relationships among benthic megafauna, are explored in **Chapter 3.** Stable isotopes of carbon and nitrogen provide a means to assess feeding strategies and trophic responses to bloom deposition, given the existence of the sediment "food bank" described in Chapter 2. These data further support the observed dampening of temporal variability in shelf sediments.

In **Chapter 4**, I test the hypothesis that the timing of settlement and recruitment in juveniles of benthic fauna would not be significantly correlated to phytodetritus deposition. Seasonal patterns in the abundance of juveniles relative to food availability are considered in the context of an ongoing debate over determinants of developmental strategy in Antarctic invertebrates.

The synthesis of research results provided in **Chapter 5** summarizes significant conclusions of the preceding chapters, and attempts to place findings in a global context by discussing relevance to climate change research. This synthesis also defines several interesting ecological questions still outstanding, and suggests possible directions for future research.

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CHAPTER 2. PERSISTENCE OF LABILE ORGANIC MATTER AND MICROBIAL BIOMASS IN ANTARCTIC SHELF SEDIMENTS: EVIDENCE OF A SEDIMENT "FOOD BANK"

ABSTRACT

The West Antarctic Peninsula (WAP) shelf experiences highly seasonal flux of particulate organic carbon following the retreat of winter sea ice, which likely results in deposition of labile food material for benthic detritivores. We conducted a seasonal time-series study (Nov 99 through Mar 01) on the WAP shelf to determine the timing and magnitude of bloom deposition on the sea floor, and the effects of seasonal deposition on microbial biomass, and persistence of labile organic material in sediments. Despite substantial seasonal changes in particle flux, the concentrations and inventories of Chl-*a* and enzymatically hydrolysable amino acids (EHAA) in near-surface sediments showed only modest seasonal variation. Interannual differences in particle flux were also large, but evidence of the elevated flux was not observed below the top 3 cm of sediment. Chl-*a* and EHAA penetrated deeply (> 5 cm) into sediments, and had long half-lives (months to years) even in high-flux summer months. These results provide evidence of a long-term sediment "food bank" for detritivores. Microbial biomass was relatively high in the top 2 cm of sediments (~1.5 to 12.4 μg ATP g^{-1} sediment), and showed only limited response to phytodetrital deposition. Despite high sediment inventories of labile organic matter and microbial biomass, rates of organic matter mineralization were in balance with sinking particle flux. We postulate that a requirement for high substrate concentrations for microbial mineralization of organic matter at low Antarctic temperatures may

promote the existence of a "food bank" of labile material in WAP shelf sediments. Further, continued climatic warming could enhance microbial remineralization of organic matter in these sediments, drawing down background levels of labile material, and altering organic-matter storage and food availability for detritivores on the WAP shelf.

INTRODUCTION

Many benthic ecosystem processes are strongly coupled to productivity patterns in the water column, both in shallow-water and deep-sea communities (Hargrave, 1973; Deuser and Ross, 1980). Recently, benthic-pelagic coupling has been studied in high-latitude oceans, where there are dramatic seasonal shifts in levels of pelagic primary production. The pulsed organic inputs to sediments resulting from spring/summer phytoplankton blooms at high latitudes may modulate carbon cycling, as well as many other processes, such as animal growth, metabolism, and selection for life histories, at the seafloor (e.g., Clarke, 1988; Grebmeier *et al.*, 1988; Grebmeier and McRoy, 1989; Ambrose and Renaud, 1995; Barnes and Clarke, 1995; Piepenburg *et al.*, 1997; Brockington *et al.*, 2001). Moreover, much of the organic carbon deposited at high latitudes during the spring/summer bloom period may be respired under winter sea-ice cover, where CO_2 efflux from sediments can be trapped beneath sea ice, entrained in newly forming deep waters, and advected into the ocean's interior (Yager *et al.*, 1995). This mechanism could play an important role in the transfer of carbon from ocean surface waters to long-term deep-sea reservoirs.

The West Antarctic Peninsula (WAP) shelf is no exception to polar seasonal productivity patterns, experiencing highly seasonal vertical flux of particulate organic carbon from summer phytoplankton blooms in December-March (Karl *et al.*, 1996), following the retreat of winter sea ice (e.g., Smith *et al.*, 1996). Sediment-trap records from the Antarctic continental shelf suggest that sinking particle flux is orders of magnitude larger during summer than during ice-covered winter months (Wefer *et al.*, 1988; Dunbar *et al.*, 1989; Honjo, 1990). This dramatic productivity pulse is likely to result in deposition of labile food material for benthic detritivores.

While bacterioplankton biomass in the WAP region has been shown to increase by nearly three orders of magnitude during the summer bloom period (Karl *et al.*, 1996), bacterial response to the summer bloom pulse has not been studied in Antarctic continental-shelf sediments. The nature of the benthic microbial response to the short-lived (4 - 8 wk long) summer bloom on the WAP shelf (e.g., Karl *et al.*, 1996) is difficult to predict. Observed correlations in deep-sea sediments between microbial biomass and metabolism, and organic carbon rain rates (Meyer-Reil and Koster, 1992; Smith *et al.*, 1997), suggest that bacterial abundance could increase in the WAP sediments during periods of POC deposition following the summer phytoplankton bloom. However, the consistently very low bottom-water temperatures in the WAP region (-2.0 – 1.0°C) could slow microbial remineralization of phytodetritus deposited on the seafloor (Pomeroy and Deibel, 1986; Pomeroy *et al.*, 1991). The combination of rapid particle sinking and low-temperature inhibition of microbial activity could lead to an accumulation of labile organic material in WAP sediments, resulting in a persistent "food bank" for benthic detritivores over long time scales relative to the water column.

The purpose of this study was to evaluate temporal dynamics of "labile" organic material in Antarctic continental shelf sediments, in an effort to test the "food bank" hypothesis. The intense seasonal particulate-flux signal observed in sediment-traps in this region was predicted to be damped in sediments due to rapid sinking and accumulation of phytodetritus at the sea floor, as well as temperature constraints on microbial metabolism. Under the "food bank" hypothesis, inventories of labile components of detritus were predicted to remain relatively constant throughout the year, such that benthic detritivores would experience substantially less seasonality in food availability than many pelagic organisms.

A seasonal time-series study was conducted on the WAP shelf, measuring sediment properties and particle flux, to determine the timing and magnitude of bloom deposition on the sea floor, as well as the effects of seasonal deposition on microbial biomass, and the concentration and turnover times of labile organic material in sediments. Results presented here, including chloropigment, labile protein, and microbial biomass data, provide evidence that labile organic pools persist on the WAP shelf over relatively long time scales of months to years (i.e., there is a sediment "food bank"). A potential role of temperature-substrate limitation on microbial metabolism in promoting the occurrence of a sediment "food bank" is suggested.

STUDY SITES

Samples were collected as part of the FOODBANCS program (Smith and DeMaster, in prep.) on a series of five twenty-two-day cruises to the West Antarctic

Peninsula (WAP) shelf (Fig. 1). In order to explore both seasonal and interannual variability in particle flux and benthic ecosystem properties, cruises were conducted over a 17-month period occurring in (I) Nov/Dec 1999 (summer pre-bloom season), (II) Mar 2000 (end of the summer bloom), (III) Jun 2000 (winter oligotrophic period), (IV) Oct 2000 (end of winter, during winter sea-ice retreat) and (V) Feb/Mar 2001 (during summer bloom) (Fig. 2). Three stations (A, B, and C) were sampled on a northwest to southeast transect across the continental shelf from Anvers Island (Fig. 1, Table 1). Two additional stations (E and F), located further south of this transect (Fig. 1, Table 1), were sampled only in Mar 2001, in order to place Stations A, B, and C into a broader regional context. Due to ice loading of the Antarctic continent, the continental shelf is generally depressed to depths in excess of 400 m (Eisma, 1988); water depth is approximately 500-650 m at all stations sampled here. Sonar and photographic surveys (C. Smith *et al.*, unpublished data) revealed little topographic relief at stations B, C, E, and F. However, Station A was located in a basin approximately 25 km wide, so topographic focusing could have impacted sediment processes in this area.

MATERIALS AND METHODS

Field methods

On each cruise, sediment cores (10-cm diameter) were collected with a Bowers & Connelly Megacorer from each of at least five randomly located deployments at each station. Overlying water was siphoned from the top of each core, and the cores were sliced into 9 discrete horizontal layers down to 10 cm, with finer 0.5-cm layers in the top

2 cm, 1.0-cm layers from 2-4 cm, and 2-cm layers below 4 cm depth. When a phytodetrital layer (greenish flocculent material with fecal pellets and intact phytoplankton cells) was visible at the surface of a core (Cruise V only), it was removed with a large plastic syringe before core slicing, and stored for separate analysis. After slicing, each layer of sediment was homogenized and divided for analysis of chloropigments, labile protein, ATP, and sediment dry-weight determinations. Sediment samples for pigment analysis were immediately frozen at -80°C and stored in the dark, while labile protein, ATP, and dry-weight samples were frozen at -20°C.

Replicate, single-cup cone-shaped sediment traps (cf., Dunbar et al. 1989) with effective mouth openings of 0.159 m^2 were deployed on Cruise I (Nov 99) at Station B. Both traps were secured on a single mooring, at 150 and 170 m above bottom. Traps were recovered and redeployed on each cruise (i.e., at 90 to 120 d intervals) until the final recovery in Mar 2001. Trap samples were preserved *in situ* with a hypersaline formalin solution (5% NaCl w/w, 10% formalin by volume), and swimmers (in particular pelagic copepods) were removed upon sample recovery using a dissecting microscope. All samples were quantitatively split, and subsamples were allocated for various analyses.

Laboratory methods

Sediment chloropigment concentrations were measured using a combination of high-performance liquid chromatography (HPLC) and fluorometric methods. Sediment-trap samples were quantitatively split, and four replicate splits from each sample were vacuum filtered through 25 mm GF/F filters. Wet filters were then placed into glass test tubes with 5 ml of 100% HPLC grade acetone, and ground with a homogenizer. Frozen sediments were thawed, and sub-samples were also placed in glass test tubes with 5 ml of acetone. All samples were vortexed, sonicated in a dark ice bath for 10 minutes, and extracted overnight in the dark at -20°C (Sun *et al.*, 1991). Extracted samples were then centrifuged at 3000 rpm for 5 min., and fluorescence of the extracts was measured at 670 nm using a Turner model 10-AU fluorometer. Each sample was extracted twice, since extraction efficiency tests indicated >95% recovery after two extractions, and concentrations for each extraction were later summed. Chloropigment and phaeopigment concentrations were calculated based on a pure Chl-*a* standard (Sigma Chemical Co.) and acidification. Values were normalized to salt-corrected dry weights of either sediment trap particulate material or the extracted sediments.

For a subset of samples (from one to three cores per station, per cruise, from phytodetritus and from sediment-trap samples), aliquots of the extracts obtained as described above were also analyzed using reverse-phase high-pressure liquid chromatography (HPLC), in an effort to verify that fluorescence values accurately represented concentrations of Chl-*a*. The HPLC system consisted of a Varian 9300 Autosampler and Varian 9012 HPLC. The column used was a 5-µm particle ODS2-Spherisorb (250 x 4.6 mm i.d.). Detection was performed using ThermoSeparations Products UV2000 and FL2000 detectors at 436 and 450 nm.

The presence of chlorophyll breakdown products or other fluorescent compounds can lead to inaccurate fluorometric measurements, particularly in sediments (Mantoura and Llewellyn, 1983; Mantoura *et al.*, 1997). In this study, fluorometric methods were found to overestimate values of Chl-*a*, and correction factors were applied to fluorometry data to obtain more accurate values for Chl-*a* concentrations in sediments. Percent differences between HPLC and fluorometric values of Chl-*a* were calculated for each of the HPLC samples (which were previously analyzed with fluorometry). Mean differences were calculated for each station at each time point. Percentages were similar for Stations B and C, and these were averaged together, giving one value for both stations at each of the five time points. Percent differences were multiplied by the fluorometric values for samples analyzed by fluorometry only, in order to correct for overestimation by fluorometry. Only corrected values are presented here. Correction factors ranged from 0.40 for phytodetrital layers to 0.015 for some layers deeper than 5 cm. Correction factors could not be obtained for sediment-trap material. Chl-*a* was not detectable in sediment trap HPLC samples because the formalin fixation altered elution times. Thus, 100 % of sediment trap fluorometric values were attributed to Chl-*a* fluorescence, since algal material deposited in traps should consist mainly of relatively fresh, intact cells.

Enzymatically hydrolysable amino acid (EHAA) analyses were performed on sediments to measure "labile protein." This assay measures an enzymatically degradable fraction of protein in sediments, which can be a relatively small percentage of the total protein pool (Dauwe *et al.*, 1999; Dell'Anno *et al.*, 2000; Danovaro *et al.*, 2001). EHAA is thought to measure the pool of protein readily available as a food source for deposit feeders (Mayer *et al.*, 1995). Frozen sediments were freeze-dried prior to amino-acid extraction. Extractions and analyses were performed according to the methods of Mayer *et al.* (1995). Briefly, soluble amino acids were extracted from replicate freeze-dried sediment samples in a poisoned phosphate buffer. One set of replicates was incubated at 37°C with Protease-K to digest the enzyme-degradable fraction. Higher molecular weight peptides were removed from all extracts via trichloroacetic acid (TCA) precipitation and centrifugation. Amino acid concentrations were obtained using the fluorescence method, in which OPA reagent was added to the lower molecular weight fraction of the extract, and fluorescence was measured on a Perkin-Elmer Model LS-5 Fluorescence Spectrophotometer ($\lambda = 340_{ex}/455_{em}$ nm). Concentrations of soluble amino acids were subtracted from values for enzyme-degraded samples to obtain EHAA concentrations. EHAA could not be measured on sediment trap samples, because formalin fixation interferes with the extraction procedure.

ATP concentrations were measured to estimate microbial biomass in sediments, although it should be noted that meiofauna could also contribute to the total ATP biomass. ATP analyses were performed according to the methods of Karl (1993). Aboard ship, six replicate, fresh sediment samples (1 cm^3) from each core slice were extracted in cold 0.5 M H_3PO_4. ATP internal standard was added to three of the six replicates to estimate adsorptive and other losses of extracted ATP (Karl and Craven, 1980; Karl, 1993). All samples were centrifuged, and 500 µl of supernatant removed to microcentrifuge tubes. Tris buffer was added to each tube, and samples were frozen at -80°C. In the laboratory, samples were stored at -20°C and thawed immediately prior to analysis. Once thawed, samples were combined with firefly lantern extract (Sigma FLE-50) prepared in a mixture of $MgSO_4$ and arsenate buffer. ATP in the extracts was then measured using the firefly luciferase-luciferin bioluminescence assay (Karl, 1993).

Statistical analyses

Data were analyzed using the Statistical Package for the Social Sciences (SPSS) software. In order to test seasonal differences in inventories of Chl-*a*, EHAA, and ATP (mass cm^{-2}), a one-way analysis of variance (ANOVA) was performed for each measurement at each sampling site (Sokal and Rohlf, 1995). Because nine discrete sediment depths were sampled with each sediment core, seasonal differences in profiles of Chl-*a*, EHAA, and ATP concentrations (mass g^{-1} sediment dry weight) were analyzed using two-factor repeated measures ANOVA (Brown *et al.*, 1997). In all tests, each sediment core was treated as a separate subject, with depth as the repeated measures factor and season as the between-subjects factor (Sokal and Rohlf, 1995). *Post hoc* pair-wise comparisons (Least Significant Difference method) were used with both one-way and repeated measures ANOVA to determine which specific seasonal interactions differed significantly.

Chlorophyll-*a* and EHAA degradation rate models

Two different models were used to estimate the degradation rate constants for Chl-*a* and EHAA in the upper 3 to 10 cm of sediment. In Model I, open-system, steady-state conditions were assumed for the ice-free summer bloom period of Nov 99 to Jun 00. The similarity of the mean Chl-*a* profiles (Fig. 4), Chl-*a* inventories (Fig. 5), and Chl-*a* flux to sediment traps across this time period indicate that Chl-*a* input to the sediments could essentially be considered constant. Model II, a non-steady-state model, was used to model Chl-*a* degradation rates based on changes in vertical flux and sediment inventories of Chl-*a* throughout the sampling period. This model was only applicable for Chl-*a* because it requires an estimate of vertical flux, which could not be obtained from sediment traps for EHAA. Both models are applied for Station B, since vertical flux values were well constrained by sediment traps at this location. The models were also applied at Station C, with the assumption that vertical flux was similar to that at Station B, given the similarity between these stations in other variables (see Results).

Under steady-state (summer) conditions, a commonly used diffusion-advection model (cf., Smith *et al.*, 1993; Stephens *et al.*, 1997; Fornes *et al.*, 1999) could be applied to obtain degradation rate constants for Chl-*a* and EHAA from sediment concentration profiles of these materials in the top 3 cm of sediment. This depth interval was chosen because the top 3 cm of sediment were consistently within the oxic zone (Hartnett and Boehme, 2005), and below 3 cm, pigment and EHAA concentrations changed little with increasing depth (i.e., $\partial C/\partial z$ was essentially zero). The model is described here in terms of Chl-*a*.

The steady-state distribution of solid phase Chl-*a* in diffusively mixed sediment, assuming constant porosity, is described by the following equation:

$$dC/dt = D_b(\partial^2 C/\partial z^2) - S(\partial C/\partial z) - kC = 0 \qquad (1)$$

where C is the concentration and k the first order degradation rate constant of Chl-*a*, t is time (yr), z is depth in sediment (cm), D_b is a bioturbation coefficient ($cm^2\ yr^{-1}$), and S is the sedimentation rate ($cm\ yr^{-1}$). Applying boundary conditions: $C(z) = C_0$ at $z = 0$, and $C \rightarrow 0$ as $z \rightarrow \infty$, leads to the following solution to Eqn. 1:

$$C = C_0 \exp(-\alpha z) \qquad (2)$$

where α^{-1} is the 1/e penetration depth of Chl-*a* (the depth at which concentration decreases to 1/e) (e.g., Stephens *et al.*, 1997). The 1/e penetration depth can be determined by curve fits to the Chl-*a* profiles, and related to k and D_b by the following:

$$\alpha = [S - (S^2 + 4kD_b)^{1/2}] / 2D_b \qquad (3)$$

D_b was calculated from profiles of excess ^{234}Th (McClintic, 2002). D_b values for the periods of interest here ranged from 1.6 to 8.2 cm^2 yr^{-1}. Modeling studies of excess ^{234}Th profiles (McClintic, 2002) indicated non-local exchange only between the sediment-water interface and depths greater than those modelled here, so non-local exchange should have had very little effect on the shape of the Chl-*a* and EHAA profiles within the top 3 cm. Sediment accumulation rates are ~30 cm ky^{-1} at Stations B and C and ~130 cm ky^{-1} at Station A (D. DeMaster *et al.*, unpublished data). Therefore, the upper limit of the bioturbation Peclet number, Pe (where Pe = SL/D_b, and L is the 3-cm depth scale of interest), is 0.24. A Pe < 1 indicates that diffusion dominates the transport processes over the depth of interest, and advection (i.e. sedimentation rate, S) can be ignored (Boudreau, 1997). Thus, Eqn. 3 can be simplified to:

$$\alpha = (k/D_b)^{1/2} \qquad (4)$$

Mean D_b values from each station on each cruise (McClintic, 2002), calculated for sediment cores collected concurrently with those used for chloropigment analysis, were used to estimate *k* (Eqn. 4) from the penetration depths determined by least-squares linear regression of log-linear plots of each chloropigment profile (Smith *et al.*, 1993).

Model II is a simple box model, in which the inventory of Chl-*a* in the top 10 cm of sediment at a given time point (t_1) is assumed to be a function of the inventory at some previous time (t_0), net vertical flux into the box since t_0 (F), and the degradation rate (k) of material within the box. A modeling depth of 10 cm was chosen in order to include the maximum depths of non-local mixing, based on excess ^{234}Th profiles (McClintic, 2002). This model was applied to sediments at Station B, where sediment traps were deployed, because the vertical flux at this station could be relatively well constrained. However, results are also presented for Station C since, as described below, similar patterns in Chl-*a* concentration were found at this station.

The rate of change in the inventory of Chl-*a* in the top 10 cm at any given time can be described by the equation:

$$dI/dt = -kI + F \tag{5}$$

where I is the inventory size (μg Chl-*a* m^{-2}) in the top 10 cm, t is time (d), k is the first-order degradation rate constant (d^{-1}), and F is the net flux of Chl-*a* into the box (i.e., sediment-trap flux in, minus burial flux out, in μg m^{-2} d^{-1}). Because burial flux of Chl-*a* was < 0.2% of sediment-trap flux (i.e., smaller than our error estimates for trap flux), burial flux was considered negligible, and thus ignored. Solving this equation gives:

$$I = [(I_0 - F/k) \exp(-kt)] + F/k \tag{6}$$

Equation 6 cannot be easily solved for k, so it's value was estimated using Matlab software's fzero function and iterative methods.

RESULTS

Vertical flux and patterns of labile organic material in sediments

Seasonal dynamics in the flux and fate of organic material in sediments was assessed by comparing Chl-*a* flux to sediment traps with temporal patterns in concentrations and inventories of chloropigments and enzymatically hydrolysable amino acids (EHAA) in sediments. Chl-*a* flux was about 21 μg m^{-2} d^{-1} throughout the spring and summer sampling periods in 1999-2000, and declined during the winter (Jun to Oct 00) to 14.5 μg m^{-2} d^{-1} (Fig. 3). A much larger flux event in the second summer season, between Oct 00 and Mar 01, yielded a summer 2001 Chl-*a* flux of 227.5 μg m^{-2} d^{-1}. This event also resulted in large interannual variability in phytodetrital accumulation between Mar 00 and Mar 01. While, at most, minimal phytodetritus appeared on the sediment surface during the first summer bloom period sampled (Mar 00), in the following summer (Mar 01), a thick phytodetrital carpet (~1-5 cm) was visible. Time-lapse photography indicates that phytodetrital deposition was greater throughout the 2000-2001 bloom season than in 1999-2000 (Suhr *et al.*, 2003; C. Smith *et al.*, unpublished data). The phytodetrital layer was removed from core surfaces and analyzed separately (Table 2).

Average Chl-*a* concentrations in sediment cores at each sampling time were similar at Stations B and C, and approximately two to four times higher at all sediment depths at Station A (Fig. 4). Sedimentation at Station A is likely to be influenced by the position of this station within a basin (Fig. 1), which may cause focusing of sedimenting organic material. Indeed, a high sediment accumulation rate at this station (130 cm ky^{-1}) relative to the outer two stations, B and C, (30 cm ky^{-1}) (D. DeMaster *et al.*, unpublished data) provides further evidence of sediment focusing. Rapid sedimentation and shallower oxygen penetration depths at Station A (Hartnett and Boehme, 2005) could also result in higher preservation efficiencies at this station (Hartnett *et al.*, 1998). Stations E and F were only sampled in Mar 01, but Chl-*a* concentrations were comparable to those at Stations B and C (Table 2).

Chl-*a* concentrations at all stations remained relatively constant throughout the year, with most temporal variability confined to the top 2 cm of sediment (Fig. 4). Concentrations in Mar 01 in the top cm of sediment were three times higher than in the previous summer (Mar 00) at Stations B and C, and nearly four times higher at Station A, coincident with the presence of phytodetritus (not included in sediment profiles; Table 2). Repeated measures ANOVA indicated significant temporal changes in the depth distribution of Chl-*a* at all three stations (Station A: $F = 4.967, p = 0.001$; B: $F = 6.897, p < 0.001$; C: $F = 5.446, p = 0.001$). At Station A, *post hoc* comparisons indicated significantly higher concentrations in Mar 01 (high flux summer) than in each of the previous four sampling periods. At Stations B and C, significant pair-wise differences were found between summer and winter seasons, and between the two successive summers (Mar 00 and Mar 01).

Inventories of Chl-*a* (μg Chl-*a* cm^{-2} of sediment surface) in the top 10 cm of sediment varied significantly across time at all stations (Station A: $F = 9.979, p < 0.001$; B: $F = 19.833, p < 0.001$; C: $F = 3.322, p = 0.029$) (Fig. 5). At Stations B and C, Chl-*a* inventories declined slightly from Nov 99 through Mar 00, yielding late summer values about 25% lower than spring values. *Post hoc* tests indicate significant differences only between particular seasons. At Station B, spring (Nov 99) and late summer (Mar 00 and Mar 01) Chl-*a* inventories were significantly higher than winter (Jun and Oct 00) inventories. The two successive summers also differed significantly from each other, indicating strong interannual variability. At Station C, inventories were significantly different between spring (Nov 99) and winter (Jun and Oct 00), and between winter (Jun and Oct 00) and the following summer (Mar 01). Seasonality was less pronounced at Station A (Fig. 5), and sediment inventories (excluding phytodetritus) remained nearly constant year-round. *Post hoc* tests verify this pattern, with significant differences occurring only between Mar 00 and Jun 00, and between Jun 00 and Mar 01. The same trends in inventory size appear when considering only the top 2 cm, or the top 4 cm of sediment (data not shown).

Chl-*a* penetrated deeply into sediments, with concentrations at 10 cm ranging from 10-50% of surface values (Fig. 4). The presence of such a readily degradable organic compound at depth suggests substantial preservation of labile material in these sediments. Modeling results indicate a low degradation rate constant (k) for Chl-*a*, implying that Chl-*a* is retained in these sediments for relatively long periods of time (Table 3). The steady-state model, based on vertical profiles of Chl-*a*, yielded values of k ranging from 0.6 to 4.6 yr^{-1} at Stations B and C. These k's yield Chl-*a* half-lives ($t_{1/2}$) for the top 3 cm of sediment on the order of 50 to 400 days for the ice-free spring and summer months at Stations B and C. The non-steady-state model, based on changes in inventory in the top 10 cm, yielded comparable results, with k for the first year ranging from a summer 2000 high of about 4 yr^{-1} to a winter low of about 1.5 yr^{-1} (Table 3). Chl-*a* half-lives derived from these values of *k* range from about 55 to 180 days. The large flux event in summer 2000-2001 resulted in a larger *k* (~11 to 15 yr^{-1}), giving a Chl-*a* half-life of about 20 days.

EHAA concentrations were similar at Stations B and C, and only slightly higher at Station A (Fig. 6), in contrast to the substantial difference in Chl-*a* concentrations between these stations. EHAA concentrations varied little with season, although at Station B, values were lower in Nov 99 than at any other period. The interannual variability observed in the Chl-*a* concentrations between Mar 00 and Mar 01 was largely absent from EHAA concentration profiles, with the exception of Station B, where a 50% increase was observed only in the surface layer (Fig. 6). EHAA inventories over the top 10 cm of sediment remained high year-round, and in general showed no statistically significant differences between seasons (Fig. 7). Results of one-way ANOVA did indicate statistically significant seasonal differences in EHAA inventory only at Station B ($F = 4.274, p = 0.013$), with *post hoc* tests revealing inventories in Nov 99 (spring) to be significantly lower than in Jun 00, Oct 00, and Mar 01.

Modeling results for EHAA degradation yielded rate constants (*k*) ranging from 0.04 to 1.25 yr^{-1} in the spring and summer at Stations B and C (Table 3). These values resulted in EHAA half-lives for ice-free seasons on the order of 6 months to 16 years.

Microbial biomass

ATP was measured in sediments and phytodetritus as an indicator of microbial biomass. Concentrations of ATP indicated very low microbial biomass below sediment depths of 3 - 4 cm (Fig. 8). ATP concentrations at most depths changed very little with season at Stations B and C; however, surface-layer values at Station C in Jun 00 and Mar 01 were more than double values in other seasons. No statistically significant differences were detected at Station B. At Station C, Oct 00 was significantly ($p < 0.05$) lower than the other four times sampled. At Station A, microbial biomass in the top 4 cm was lowest in spring and summer (Nov 99 and Mar 00), increasing steadily through the winter to a maximum in Oct 00. Significant differences ($p < 0.05$) in ATP concentration profiles were detected at Station A, with Nov 99 less than Jun 00, and Jun 00 less than Mar 01. Biomass concentrations in surface sediments did not show the same interannual variability as Chl-*a*, with ATP concentrations similar in Mar 00 and Mar 01 (Fig. 8). However, note that the concentration of microbial biomass in Mar 01 in the phytodetrital layer was 4 to 10 times higher than in surface sediments at all stations (Table 2).

ATP inventories within the sediments (i.e., excluding phytodetritus) at Station A were largest in the winter, increasing approximately 30% from Nov 99 to Jun 00, and then declining steadily to about 50% of the Jun 00 value by Mar 01 (Fig. 9). ATP inventories did show a statistically significant seasonal trend at Station A ($F = 3.216, p = 0.036$), with significant *post hoc* comparisons generally found between summer and winter. Again, despite the higher flux of Chl-*a* in Mar 01, microbial biomass inventories within sediments were smaller in Mar 01 than the previous summer, suggesting a time lag between phytodetritus deposition and buildup of peak microbial biomass *within* the sediments. However, when the contribution to the inventory of the phytodetrital layer in Mar 01 is considered, values are comparable to Mar 00. At Stations B and C, ATP inventories declined by about 80% from Nov 99 to Oct 00, and then increased again in

Mar 01, especially when the phytodetrital layer is included (Fig. 9). This trend mirrors that of the Chl-*a* inventories at Stations B and C. Significant differences in inventory size were found at Station C ($F = 3.759, p = 0.024$), with Oct 00 less than both Nov 99 and Mar 00. No significant differences were found at Station B, due to large within-site variance (Fig. 9). Notably, the presence of phytodetritus in Mar 01 increased ATP inventories at all three primary stations (A, B and C) in a pattern even more dramatic than for Chl-*a*.

DISCUSSION

As anticipated, our results indicate significant seasonal variability in vertical flux of Chl-*a* to the WAP shelf (Fig. 3). However, interannual differences in flux were far greater than seasonal differences during our study period. Despite the large temporal variability in flux, seafloor concentrations and inventories of labile compounds such as Chl-*a* and EHAA varied modestly, particularly below the top few centimeters of sediment. Microbial biomass also varied only slightly with season, with most of the variability confined to the top 3 to 4 cm and the phytodetrital layer. Further, the large flux event in 2000-2001 had not stimulated a concomitant increase in sediment microbial biomass by the time of our sampling in late summer (Mar) 2001.

Evidence of a sediment "food bank"

To evaluate the presence of a sediment food bank, it is necessary to compare changes in sediment inventories to the high temporal variability in particle flux to the

WAP shelf. Sediment traps deployed during this study yielded seasonal flux estimates ranging from 1.2 mmol C_{org} m^{-2} d^{-1} in summer 1999 to 0.5 mmol C_{org} m^{-2} d^{-1} in winter 2000 (C. Smith and D. DeMaster, unpublished data), and Chl-*a* fluxes varied similarly with season. However, interannual variability between the two summer bloom periods sampled was even greater than seasonal variability, with a 5-fold difference in C_{org} flux (C. Smith and D. DeMaster, unpublished data) and more than a 10-fold difference in Chl-*a* flux (Fig. 3) between Mar 00 and Mar 01. Comparison of shallow (D. Karl *et al.*, unpublished data) versus our deep-moored sediment trap fluxes indicates very little recycling of surface production in the water column between 150 and 450 m depth on the WAP shelf. Thus, the flux of summer bloom-derived phytodetritus is likely to constitute a relatively undegraded, yet temporally varying, input of food for shelf benthos.

Evidence of high-quality detritus rapidly reaching the deep shelf floor has been reported in other Antarctic studies (Dunbar *et al.*, 1998; Fileman *et al.*, 1998), and for numerous deep-sea sites (e.g., Billett *et al.*, 1983; Lampitt, 1985; Smith *et al.*, 1996; Fabiano *et al.*, 2001; Beaulieu, 2002). Many studies, especially at mid-latitudes, have also demonstrated a coupling between pelagic and benthic processes, whereby benthic organic matter accumulation and metabolism are linked to flux events derived from phytoplankton blooms in the upper ocean (e.g., Gooday and Turley, 1990; Graf, 1992; Ambrose and Renaud, 1995; Pfannkuche *et al.*, 1999). We hypothesized that the coupling between phytodetritus deposition and mineralization would be relatively weak on the WAP shelf because phytodetritus would be rapidly mixed into sediments by active bioturbation, and degraded slowly (over periods of months) at the very low water temperatures, leading to storage of bloom material in a sediment "food bank." If the food bank hypothesis is correct, labile organic matter pools in sediments should be present year-round, despite very low sinking organic flux from the water column during ice-covered winter months.

Profiles (Fig. 4) and inventories (Fig. 5) of Chl-*a*, a commonly used tracer of fresh phytoplankton biomass (Furlong and Carpenter, 1988; Sun *et al.*, 1991; Sun *et al.*, 1994; Stephens *et al.*, 1997), indicate moderate seasonal changes in phytoplankton detritus in WAP sediments. Despite the high degree of interannual variability in particle flux (in particular, a thick phytodetrital carpet in Mar 01), Chl-*a* concentrations in sediments below the top 1 cm varied little at most of our stations (Fig. 4). EHAA concentration profiles and inventories (Figs. 6 and 7) exhibited even less temporal variability than chloropigments; seasonal changes were minimal, and dramatic increases in EHAA concentrations beneath the phytodetrital layer in Mar 01 were not observed. The proportion of the EHAA inventory contained in the phytodetrital layer was also quite small (Fig. 7). While inputs of fresh phytodetritus are often strongly correlated with chloropigment concentrations in sediments, our results, and those of others, suggest that *labile protein accumulation* is not necessarily strongly coupled to phytodetrital input (Fabiano *et al.*, 2001; Demopoulos *et al.*, 2003).

Chl-*a* and EHAA are not only available in sediments on the WAP shelf year-round, they are relatively enriched compared to other marine sediments. Chl-*a* concentrations ranged from about 6 to 50 ng g^{-1} in surface sediments from the equatorial Pacific (Smith *et al.*, 1996; Stephens *et al.*, 1997), from 80 to 900 ng g^{-1} in North Carolina slope sediments (600-800 m) (Cahoon *et al.*, 1994), and from ~100 to 150 ng g^{-1} in shallow (28 m) North Sea sediments during the summer maximum (Boon and

Duineveld, 1998). These values are moderate to low when compared to our values of 250 to 1000 ng g^{-1} for the WAP shelf, and for shelf stations in the Ross Sea, Antarctica (Fabiano and Danovaro, 1998). Baldwin and Smith (2003) report even higher Chl-*a* concentrations of 1000 to 14,000 ng g^{-1} for surface sediments in the enclosed bay of Deception Island, Antarctica. However, these latter values are based solely on fluorometry, which may overestimate Chl-*a* concentration in sediments (Mantoura and Llewellyn, 1983; Mantoura *et al.*, 1997).

EHAA values from surface sediments on the WAP shelf are also relatively high at 0.5 to 0.75 mg g^{-1}, compared to a range of ~0.1 to 0.5 mg g^{-1} for samples from shelf depths in the North Sea, bathyal basins off California, and abyssal depths in the Porcupine Abyssal Plain (Dauwe *et al.*, 1999; Dell'Anno *et al.*, 2000; Danovaro *et al.*, 2001; Demopoulos *et al.*, 2003).

Persistence of Chl-*a* and EHAA in WAP shelf sediments is increasingly apparent when the concentrations of these tracers are normalized to the organic carbon (C_{org}) content of the sediments. The Chl-*a*:C_{org} and EHAA:C_{org} ratios are moderate to high in WAP shelf sediments, with Chl-*a*:C_{org} reaching 10^{-4} in the top centimeter of sediment. Chl-*a*:C_{org} in Deception Island sediments was also on the order of 10^{-4} (Baldwin and Smith, 2003), although, as mentioned above, Chl-*a* values in that study could be substantially overestimated by fluorometric methods. While Demopoulos *et al.* (2003) found similar Chl-*a*:C_{org} ratios in California's bathyal basins, their Chl-*a* concentrations are also based on fluorometry, and are thus likely overestimates as well. Chl-*a*:C_{org} ratios in abyssal equatorial Pacific sediments, with <1% C_{org}, were at least an order of magnitude smaller than in WAP shelf sediments, measuring about 2 x 10^{-5} (C. Smith *et* *al.*, 1996). EHAA:C_{org} ratios in WAP shelf surface sediments ranged from about 0.03 to 0.08, whereas Demopoulos *et al.* (2003) report ratios up to an order of magnitude lower (0.009 to 0.02) in bathyal basins off California. EHAA:C_{org} at 280-m depths in the North Sea (0.019) also fell below WAP shelf values (Dauwe *et al.*, 1999). These relatively high ratios in WAP sediments suggest that high proportions of depositing Chl-*a* and EHAA are retained in surficial sediments in this region. The relatively low organic carbon content (1%) in WAP shelf sediments appears to result from dilution of labile detritus by deposition of inorganic mineral components (McClintic, 2002), rather than from rapid degradation of summer bloom detritus.

Unexpectedly, substantial Chl-*a* and EHAA concentrations were detected down to the deepest depths (10 cm) sampled in this study. Half-lives ($t_{1/2}$) for Chl-*a* in oxic sediments vary widely, but laboratory experiments with shallow-water sediments have yielded values on the order of 10 to 30 days (Sun *et al.*, 1993). However, much longer degradation half-lives (weeks to months) have been observed by other researchers in cold, and deepwater habitats (Stephens *et al.*, 1997; Josefson *et al.*, 2002). In the present study, the half-life for Chl-*a* in the sediment mixed layer ranged from roughly 50 to 200 days (Table 3), even in the oxic top 3 cm of sediment. ^{14}C measurements from this study also estimate labile carbon turnover times at 90 to 240 days (DeMaster *et al.* 2003). Some reports of long Chl-*a* half-lives result from diagenetic modeling of deeper, anoxic sediments, where Chl-*a* degradation is slowed (e.g., Sun *et al.*, 1993; Stephens *et al.*, 1997). However, the Chl-*a* profiles modelled here only extended to 3 cm, and were well within the oxygenated surface sediments (Hartnett *et al.*, 2005). Alternatively, slow Chl-*a* degradation rates found on the WAP shelf may be related to low Antarctic bottom water temperatures. Sun *et al.* (1993) reported a fourfold decrease in k as experimental temperatures were lowered from 25 to 5°C, with a half-life of 31 d at 5°C. Thus, lower degradation rates might be expected on the WAP shelf, where bottom water temperatures drop as low as –1.8°C.

Because degradation rates of EHAA have not been reported elsewhere, we cannot be certain that EHAA degradation in WAP sediments, with half lives of months to years, is unusually slow (Table 3); however, the high EHAA concentrations and EHAA:C_{org} ratios suggest strongly that this is the case. While the EHAA assay is designed to simulate digestion in a deposit feeder gut, and is thought to extract the most "labile" protein fraction (Mayer *et al.*, 1995), the long half-lives indicate that EHAA may not be a sensitive measure of newly deposited phytoplankton detritus, at least in Antarctic shelf sediments. A study of detritivore food quality in California borderland basins also suggested different (e.g., slower) degradation dynamics for EHAA than for Chl-*a* (Demopoulos *et al.*, 2003). Nonetheless, substantial evidence supports the usefulness of EHAA concentration as a measure of detritivore food quality, i.e. as an indicator of a sediment "food bank" (Mayer *et al.*, 1995; Dauwe *et al.*, 1999; Pusceddu *et al.*, 2003). Thus, while EHAA appears to be a useful measure of the quantity of reactive organic material available as food to detritivores, seasonal variability in the vertical flux of EHAA associated with phytoplankton detritus is likely to be damped in WAP sediment inventories.

While some seasonal changes are evident in sediment chloropigment values, they are clearly less pronounced than interannual changes. Without additional sampling following the high-flux event in summer 2001, we cannot determine the long-term effects on sediment inventories of interannual, relative to seasonal, variability in particulate flux. However, fairly sizable pools of labile material do persist in WAP shelf sediments, indicating substantial sedimentary "inertia" which dampens the effects of extreme temporal variability in productivity of the overlying waters. Normally labile material appears to degrade slowly in these sediments, such that unusually large flux events could have long-lasting effects on sediment inventories, producing a sediment "food bank" for detritivores.

Microbial response to phytodetritus deposition

Changes in microbial biomass inventories (Fig. 9) roughly mimic those of chloropigment inventories (Fig. 5) at Stations B and C, with steady declines from a secondary maximum at the initial break-up of pack ice (Nov 99) to a late-winter minimum (Oct 00). This pattern suggests a stimulation of microbial growth by the summer bloom at these two outer stations, and a subsequent decline in biomass as labile material is degraded. In contrast, microbial biomass at Station A exhibited a delayed response to the summer bloom, increasing steadily after the bloom and into the winter. This decoupling of vertical flux and microbial growth could be the result of non-seasonal inputs of organic material via lateral advection or topographic focusing in the relatively complex basin at Station A.

While some seasonal changes in microbial biomass do occur in WAP shelf sediments, they are substantially smaller in magnitude than those occurring in the water column. Microbial biomass inventories varied seasonally in WAP shelf sediments by approximately three-fold or less, whereas bacterioplankton abundances in WAP surface waters increase as much as six fold from winter to summer months (Karl *et al.*, 1996; Church *et al.*, 2003). The relatively low resolution sampling time-series conducted here (Fig. 2) may have missed any short-lived (<60 days) increases in microbial biomass in response to brief deposition events, particularly in summer 1999/2000 when no phytodetrital carpet was observed in sediment samples. However, time-lapse photographs of the seafloor taken every 12 hours throughout the entire 17-month field program did not show any evidence of flux events occurring between sampling time points (C. Smith *et al.*, in prep.). Thus, the relative lack of seasonal variability in seafloor inventories of labile components of detritus and microbial biomass do not appear to be sampling artifacts.

Seasonal trends in microbial biomass at stations B and C were not matched by sediment-community respiration rates, which showed no statistically significant seasonal variation (Thomas *et al.*, 2005). However, WAP shelf respiration rates were moderately high relative to other shelf and deep-sea settings (e.g., Gage and Tyler, 1991; Boon and Duineveld, 1998; Smith *et al.*, 2001; Smith and Demopoulos, 2003), and roughly balanced the flux minus burial of sedimenting organic material (D. DeMaster *et al.*, unpublished data). Similar measurements in shallow Arctic and Antarctic waters also indicate a broad balance between carbon flux and benthic remineralization (Nedwell *et al.*, 1993; Boon and Duineveld, 1998). Given this balance between POC flux and mineralization, as well as the presence of a large, metabolically active microbial community on the Antarctic shelf, why do pools of labile organic matter (e.g., Chl-*a* and EHAA) persist at high concentrations?

Temperature-substrate limitation hypothesis

The persistence of large pools of labile organic matter in WAP sediments may be explained by a requirement for high substrate concentrations to drive microbial mineralization activities at very low temperatures (Pomeroy and Deibel, 1986; Wiebe *et al.*, 1993; Yager and Deming, 1999; Nedwell, 1999; Pomeroy and Wiebe, 2001). A number of studies suggest that at low temperatures, microbial communities may require higher substrate concentrations to sustain a particular level of heterotrophic activity (Pomeroy and Deibel, 1986; Pomeroy *et al.*, 1991; Wiebe *et al.*, 1992; Wiebe *et al.*, 1993; Nedwell and Rutter, 1994; Arnosti *et al.*, 1998; Arnosti and Jorgensen, 2003). Despite this evidence, the nature of temperature effects on microbial activity has remained controversial. Viable microbial communities are known to exist in glacial ice and permafrost soils, surviving at very low temperatures (down to -40°C) (e.g., Price and Sowers, 2004 and references therein). However, these communities survive through extremely low metabolic rates sufficient to maintain the cellular environment. Indeed, the potential for low temperatures to limit the rates of diffusion-dependent microbial processes seems intuitive (cf., Jumars *et al.*, 1993). Despite the effects of temperature on microbial metabolism, sediment community respiration rates in Antarctic sediments (e.g., Nedwell *et al.*, 1993; Thomas *et al.*, 2005) are comparable to those in other bathyal and shelf environments (reviewed in Levin and Gooday, 2003; Smith and Demopoulos, 2003). Here we propose a simple conceptual model whereby seemingly conflicting reports of high sediment community respiration rates and low microbial activity in cold temperatures can be reconciled.

Organic material in marine sediments is largely composed of high molecular weight compounds not readily available for bacterial uptake, which must be hydrolyzed outside the cell by extracellular enzymes. We suggest that temperature effects on the activity of these enzymes can potentially limit microbial metabolic rates in Antarctic shelf sediments. According to substrate addition experiments in natural, low-temperature microbial communities, extracellular enzymatic hydrolysis is potentially rapid at high (i.e., saturating) concentrations of substrate, both in polar shelf sediments (Arnosti *et al.*, 1998; Fabiano and Danovaro, 1998) and in the deep sea (Meyer-Reil and Koster, 1992; Boetius and Lochte, 1996). Further, the temperature optima of at least some of the enzymes from permanently cold sediments are significantly higher than ambient environmental temperatures, and warming of the sediment greatly increases extracellular enzyme activity (EEA) at sub-saturating concentrations of substrate (Meyer-Reil and Koster, 1992; Nedwell and Rutter, 1994; Arnosti and Jorgensen, 2003). Thus, it appears that extracellular hydrolysis is not inherently limited by low temperature if sufficient (i.e., high) levels of substrate are available.

A requirement for higher substrate concentrations at low temperatures suggests decreased affinity of extracellular enzymes for substrate binding, and/or reduced affinity of membrane-bound transport proteins for substrate uptake across cell membranes at low temperatures (Nedwell, 1999). Enzyme affinity has been described for Antarctic bacteria using Michaelis-Menten enzyme kinetics, which relates growth rate to substrate concentration (e.g., Nedwell and Rutter 1994; Gerday *et al.*, 1999). For Antarctic bacterial isolates, specific affinity for particular substrates, $a°_A$ (where $a°_A = \mu_{max} K_s^{-1}$, with μ_{max} the maximum growth rate and K_s the Michaelis-Menten half-saturation constant), appears to decline with temperature (Reay *et al.*, 1999). These results, and similar data from some Arctic bacterioplankton (Yager and Deming, 1999), suggest an increased limitation of bacterially mediated mineralization rates by low substrate concentrations when temperatures are low.

It seems quite reasonable that microbial mineralization and respiration of a given type of organic substrate in sediments is limited by EEA, such that the rate of hydrolysis is a product of substrate concentration (S) and a reaction rate constant (κ). Ultimately, total microbial heterotrophic activity is limited by the sum of the products of substrates and characteristic κ values. In other words, sediment community respiration, R, can be described by the equation:

$$R \propto \Sigma(S_i\, \kappa_i)$$

where S_i and κ_i are the respective concentrations and reaction-rate constants for the metabolizable components of the sediment organic matter. This formulation is conceptually identical to the oft-cited "G-model" of Berner (1980, Nedwell, 1984) and the "multi-B" model of Smith *et al.* (1994). The value of a particular κ_i is related to enzyme efficiency, which, according to the studies discussed above, decreases at low temperature. As a given κ_i decreases due to lower temperatures, substrate conversion rate can be maintained for a given quantity of enzyme only by enhancement of substrate concentration (S_i). Thus, we hypothesize that at low temperatures, a higher S may be required to maintain a particular community-level rate of organic matter breakdown (κS) via enzymatic hydrolysis. WAP sediments might be thought of as operating at high average S and low average κ (Fig. 10), as might Arctic shelf sediments (note the strong negative relationship between temperature and sediment organic content in Glud *et al.*'s (1998) Arctic shelf data). The mineralization of organic matter in tundra soils appears to follow similar high *S*, low κ dynamics (Schlesinger, 1997). Low average *S* and high κ, in contrast, would be characteristic of tropical and temperate sediments.

According to the temperature-substrate limitation hypothesis, the ability of bacteria to utilize organic material at low concentrations in sediments would be greatly reduced at the low temperatures typical of Antarctic shelf waters. Thus, organic matter would tend to build up in sediments until high enough substrate concentrations were achieved to allow community respiration to balance the sinking flux of labile POC. As a consequence, relatively high steady-state organic matter concentrations, such as those seen here for Chl-*a* and EHAA, would be expected to accumulate in very cold sediments. Periodic deposition events should allow for short-term increases in microbial activity, while high background levels of organic matter persist in the long-term. In temperate areas, total microbial community respiration rates may be equivalent, but concentrations of labile organic matter should be "burned" down by microbial metabolism to lower steady-state levels. Further, a more intense response to organic flux events would be expected in temperate sediments, because pulses of labile organic material can be respired to lower concentrations.

The increasing steepness of the relationship between hydrolytic enzyme efficiency and temperature at very low temperatures (<2°C) (e.g., Arnosti and Jorgensen, 2003) suggests that warming of Antarctic shelf bottom waters by a few degrees could significantly enhance the efficiency of microbial remineralization, drawing down background levels of labile organic material in sediments. This in turn could reduce food availability for benthic detritivores by decreasing the size of the “food bank”, altering food webs and reducing the rate of carbon sequestration in Antarctic shelf sediments. If the temperature-substrate limitation hypothesis is correct, continuation of the current trend of climate warming in the Antarctic Peninsula region (R. Smith *et al.*, 2003) could have unexpectedly rapid impacts on benthic ecosystem function.

Table 1. Position and approximate water depth of all stations sampled.

Station	Lat	Long	Depth (m)
A	65° 10.32’ S	64° 47.0’ W	490
B	64° 48.0’ S	65° 21.0’ W	610
C	64° 12.5’ S	65° 21.9’ W	560
E	65° 58.84’ S	67° 17.26’ W	615
F	66° 54.08’ S	69° 39.8’ W	670

Table 2. Average Chl-*a*, EHAA and ATP concentrations, C/N ratios, porosity, and wt. % organic carbon in surface sediments (0-0.5 cm) and phytodetritus (Mar-01 only) for Sites A, B, C, E and F. Values represent the means of 3 to 5 samples, ± one standard error; where no errors are given, only one sample was analyzed.

Location	Sampling Date	Chl-*a* (µg/g)	EHAA (mg/g)	ATP (µg/g)	C/N (wt/wt)	Porosity (vol/vol)	% Org C (mg/mg)
Site A	Nov-99	1.29 ± 0.2	0.64 ± 0.1	2.27 ± 0.4	6.8 ± 0.08	0.74 ± 0.02	1.17 ± 0.02
(0-0.5 cm)	Mar-00	0.75 ± 0.07	0.70 ± 0.07	5.04 ± 2.4	6.8 ± 0.05	0.68 ± 0.07	1.34 ± 0.01
	Jun-00	0.94 ± 0.07	0.54 ± 0.02	9.49 ± 3.05	7.0 ± 0.05	0.67 ± 0.1	1.25 ± 0.001
	Oct-00	0.57 ± 0.05	0.62 ± 0.1	12.43 ± 0.4	6.7 ± 0.2	0.75 ± 0.04	1.26 ± 0.06
	Mar-01	3.07 ± 0.6	0.68 ± 0.1	4.00 ± 1.2	6.3 ± 0.3	0.71 ± 0.1	1.46 ± 0.1
Phytodetritus		83.93 ± 39.0	1.00 ± 0.3	32.34 ± 24.4	5.9 ± 0.6	0.83 ± 0.06	1.70 ± 0.3
Site B	Nov-99	0.32 ± 0.07	0.32 ± 0.04	2.08 ± 0.8	7.4 ± 0.7	0.80 ± 0.05	1.05 ± 0.06
(0-0.5 cm)	Mar-00	0.23 ± 0.02	0.45 ± 0.05	2.48 ± 0.8	6.7 ± 0.1	0.58 ± 0.07	1.03 ± 0.02
	Jun-00	0.17 ± 0.03	0.51 ± 0.07	1.57 ± 1.3	n.d.	0.60 ± 0.07	n.d.
	Oct-00	0.15 ± 0.01	0.58 ± 0.03	1.42 ± 0.07	n.d.	0.74 ± 0.04	n.d.
	Mar-01	0.72 ± 0.2	0.71 ± 0.2	3.58 ± 1.04	6.1 ± 0.3	0.77 ± 0.03	1.90 ± 0.7
Phytodetritus		4.95 ± 0.9	1.27 ± 0.2	42.29 ± 8.1	6.2 ± 0.03	0.80 ± 0.07	1.14 ± 0.08
Site C	Nov-99	0.45 ± 0.06	0.51 ± 0.02	1.99 ± 0.7	6.8 ± 0.2	0.67 ± 0.04	1.11 ± 0.08
(0-0.5 cm)	Mar-00	0.24 ± 0.03	0.64 ± 0.09	2.29 ± 0.5	6.7 ± 0.01	0.81 ± 0.04	1.09 ± 0.07
	Jun-00	0.31 ± 0.04	0.44 ± 0.09	5.31 ± 2.8	6.5 ± 0.06	0.65 ± 0.06	1.07 ± 0.03
	Oct-00	0.13 ± 0.02	0.46 ± 0.04	1.85 ± 0.7	6.6 ± 0.06	0.81 ± 0.03	0.97 ± 0.03
	Mar-01	0.79 ± 0.2	0.57 ± 0.09	5.77 ± 2.5	6.0	0.82 ± 0.03	1.19
Phytodetritus		1.42 ± 0.3	0.64 ± 0.3	19.76 ± 13.3	5.7	0.83 ± 0.1	0.93 ±0.002
Site E	Mar-01	1.12 ± 0.7	n.d.	n.d.	n.d.	0.90	n.d.
Phytodetritus		8.53 ± 3.7	n.d.	n.d.	n.d.	1.01	n.d.
Site F	Mar-01	0.37 ± 0.07	n.d.	n.d.	n.d.	0.89 ± 0.2	n.d.
Phytodetritus		2.17 ± 0.2	n.d.	n.d.	n.d.	0.84 ± 0.03	n.d.

Table 3. Results of Chl-*a* and EHAA degradation rate models. Model I (open-system, steady-state) is based on concentration profiles of Chl-*a* and EHAA for the top 3 cm of sediment for spring/summer 1999-2000. Model II (non-steady-state box model) is based on sediment trap fluxes and inventories of Chl-*a* for the top 10 cm of sediment. Values of D_b are the bioturbation rates (cm^2 yr^{-1}) obtained from profiles of $^{234}Th_{xs}$ in the top 3 cm of sediment, and used only for Model I calculations of degradation rate constants (k). Model I values are ± 1 standard error (N = 3 to 5).

Model	Material	Date	D_b	k (yr^{-1})	$t_{1/2}$ (yr)
I	Chl-*a*	Nov 99	6.09 ± 3.91	2.49 ± 0.38	0.28 ± 0.12
Station B		Mar 00	2.93 ± 0.062	1.20 ± 0.004	0.58 ± 0.18
		Jun 00	5.72 ± 2.55	4.33 ± 0.16	0.16 ± 0.02
	EHAA	Nov 99	6.09 ± 3.91	0.45 ± 0.094	1.54 ± 0.31
		Mar 00	2.93 ± 0.062	0.15 ± 0.004	4.50 ± 3.75
		Jun 00	5.72 ± 2.55	0.19 ± 0.14	3.68 ± 11.52
I	Chl-*a*	Nov 99	10.03 ± 4.97	4.57 ± 0.41	0.15 ± 0.06
Station C		Mar 00	3.12 ± 0.95	0.57 ± 0.05	1.21 ± 0.27
		Jun 00	6.19 ± 4.14	4.59 ± 0.27	0.15 ± 0.03
	EHAA	Nov 99	10.03 ± 4.97	0.28 ± 1.26	2.50 ± 4.32
		Mar 00	3.12 ± 0.95	0.043 ± 0.041	16.09 ± 15.82
		Jun 00	6.19 ± 4.14	1.25 ± 1.13	0.56 ± 1.72
II	Chl-*a*	Nov 99-Mar 00	N/A	3.25	0.21
Station B		Mar 00-Jun 00		4.56	0.15
		Jun 00-Oct 00		1.42	0.49
		Oct 00-Mar 01		11.53	0.06
II	Chl-*a*	Nov 99-Mar 00	N/A	2.15	0.32
Station C		Mar 00-Jun 00		3.87	0.18
		Jun 00-Oct 00		1.90	0.37
		Oct 00-Mar 01		14.78	0.05

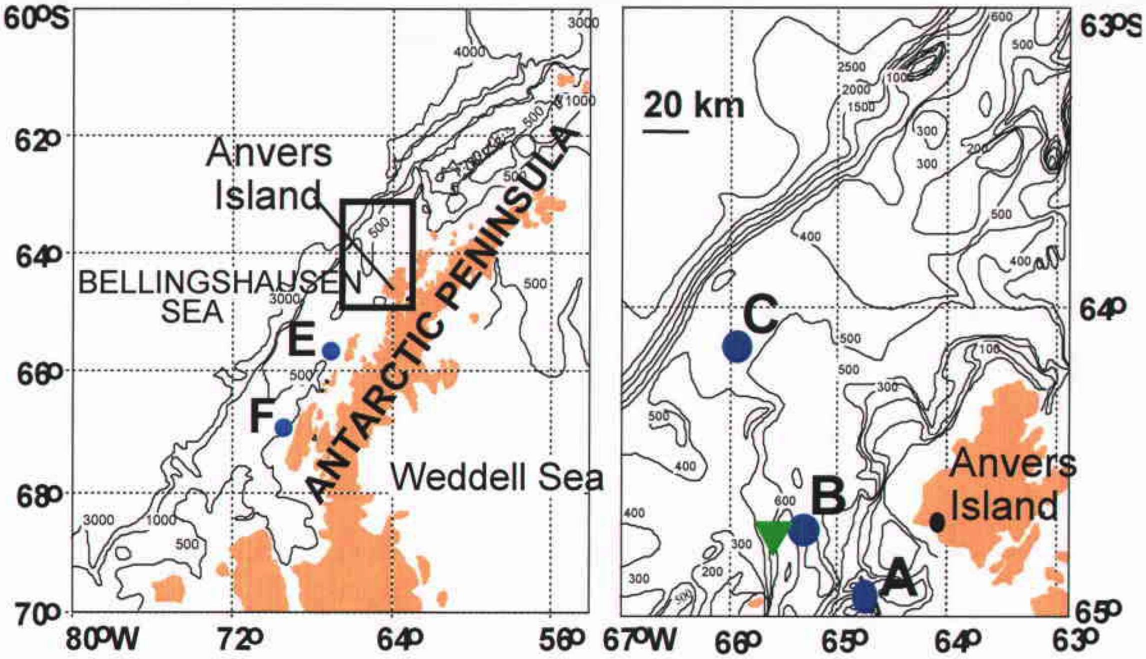
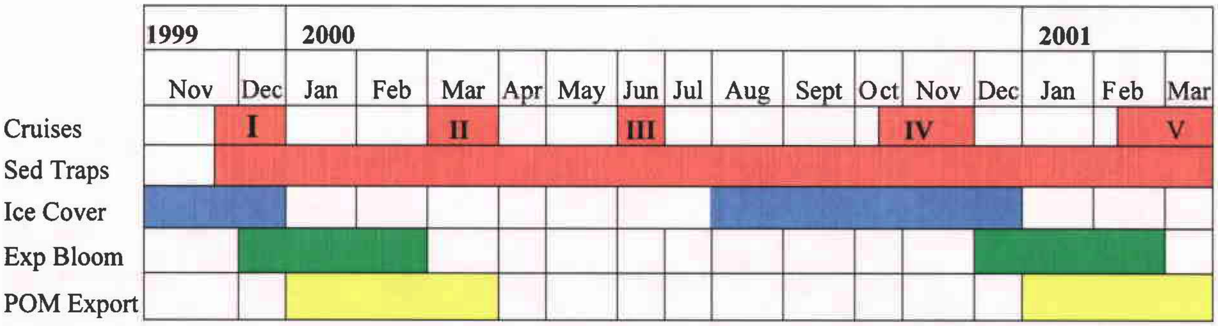


Fig. 1. Map of the study area. (●) Locations of Stations A, B, C, E, and F; (▼) Location of sediment trap mooring.



	1999		2000											2001		
	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar
Cruises		🟥 I			🟥 II			🟥 III				🟥 IV	🟥			🟥 V	🟥
Sed Traps		🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥
Ice Cover	🟦	🟦								🟦	🟦	🟦	🟦	🟦			
Exp Bloom		🟩	🟩	🟩										🟩	🟩	🟩	
POM Export			🟨	🟨	🟨										🟨	🟨	🟨

Fig. 2. Sampling time-line indicating timing of cruises relative to ice cover, expected summer bloom occurrence, and periods of maximum, bloom-derived POM export.

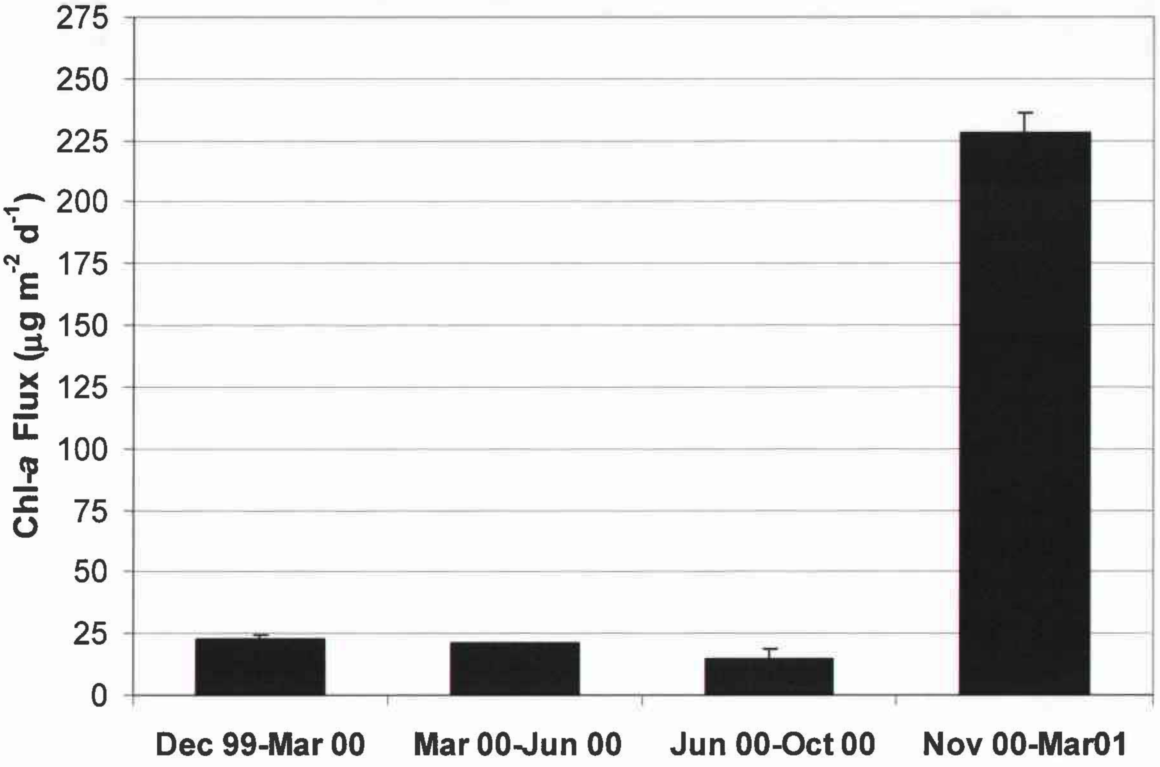


Fig. 3. Mean Chl-*a* mass flux (µg m^{-2} d^{-1}) measured in two in-line sediment traps moored at 150 and 170 m above bottom at Station B. Error bars are ± 1 standard error.

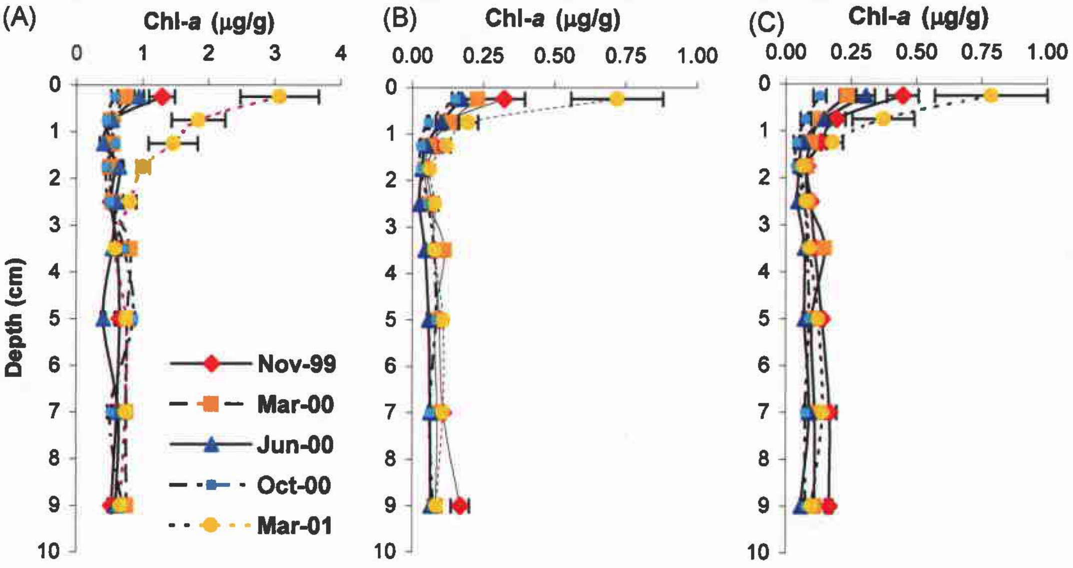


Fig. 4. Sediment Chl-*a* concentration (µg Chl-*a* g^{-1} sediment dry weight) in top 10 cm at (A) Station A; (B) Station B; (C) Station C. Concentration of Chl-*a* in phytodetritus is not included in the surface sediment value. Note the different scales between (A) and (B) and (C). Each profile represents mean concentration (N = 5). Error bars are ± 1 standard error.

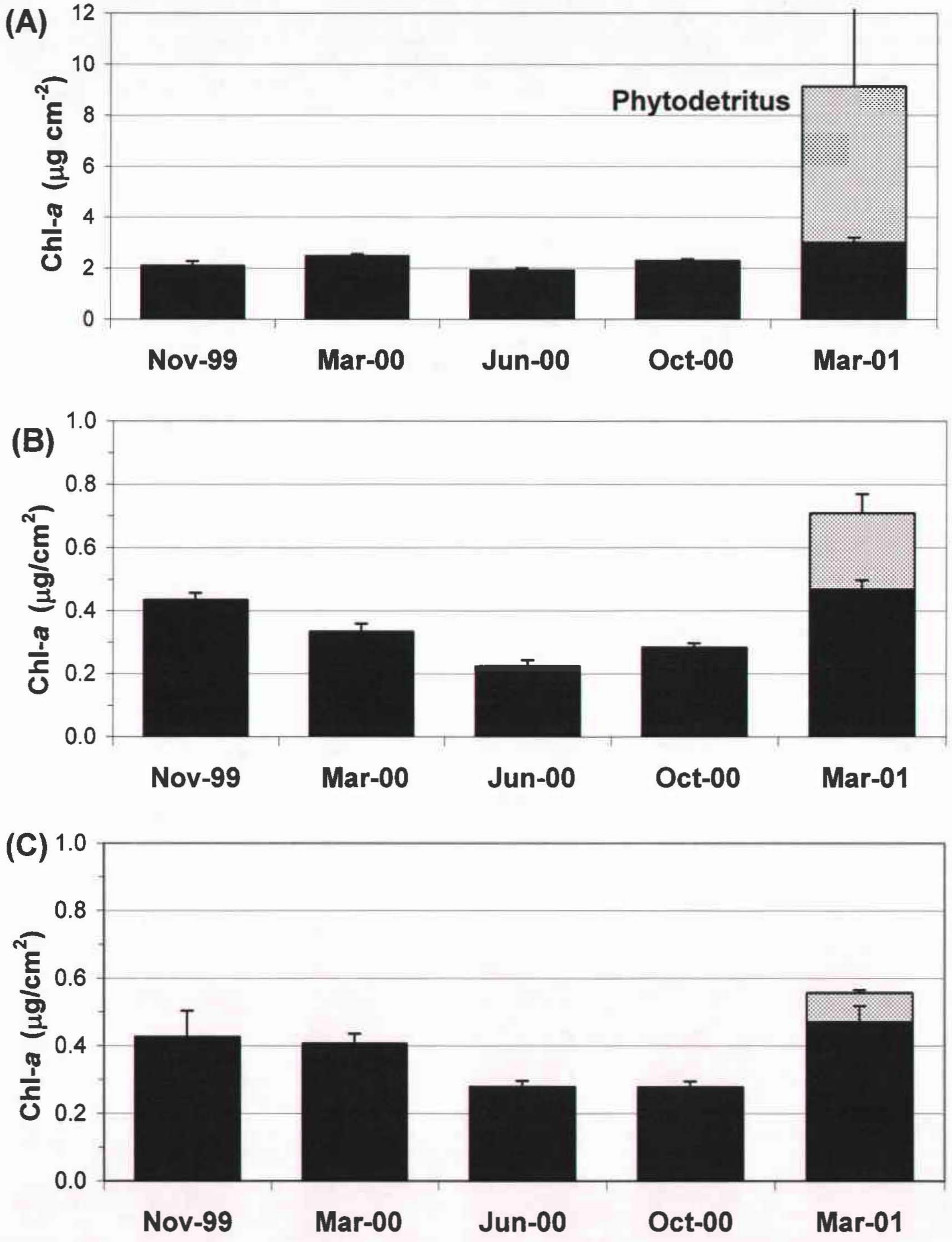


Fig. 5. Inventory of Chl-*a* (μg cm^{-2}) in top 10 cm of sediment at (A) Station A; (B) Station B; (C) Station C. The stippled portion of the Mar-01 bar in each figure represents the μg Chl-*a* cm^{-2} in the phytodetrital layer. Note the difference in scale between Fig. (A) and Figs. (B) and (C). N = 5 cores per time point. Error bars are ± 1 standard error.

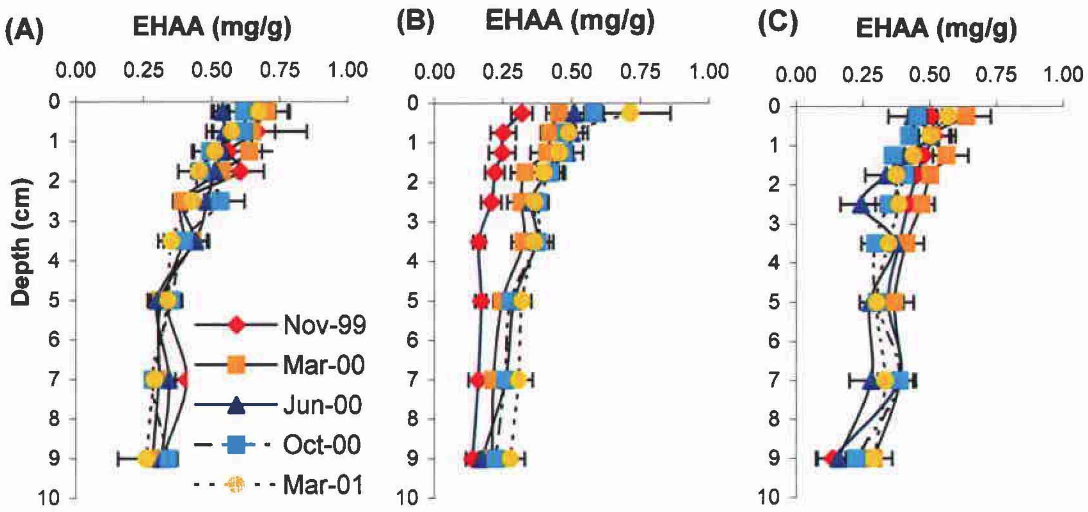


Fig. 6. Sediment EHAA concentration (mg EHAA g^{-1} sediment dry weight) in top 10 cm at (A) Station A; (B) Station B; (C) Station C. Concentration of EHAA in phytodetritus is not included in the surface sediment value. Each profile represents mean concentration (N = 3 to 5). Error bars are ± 1 standard error.

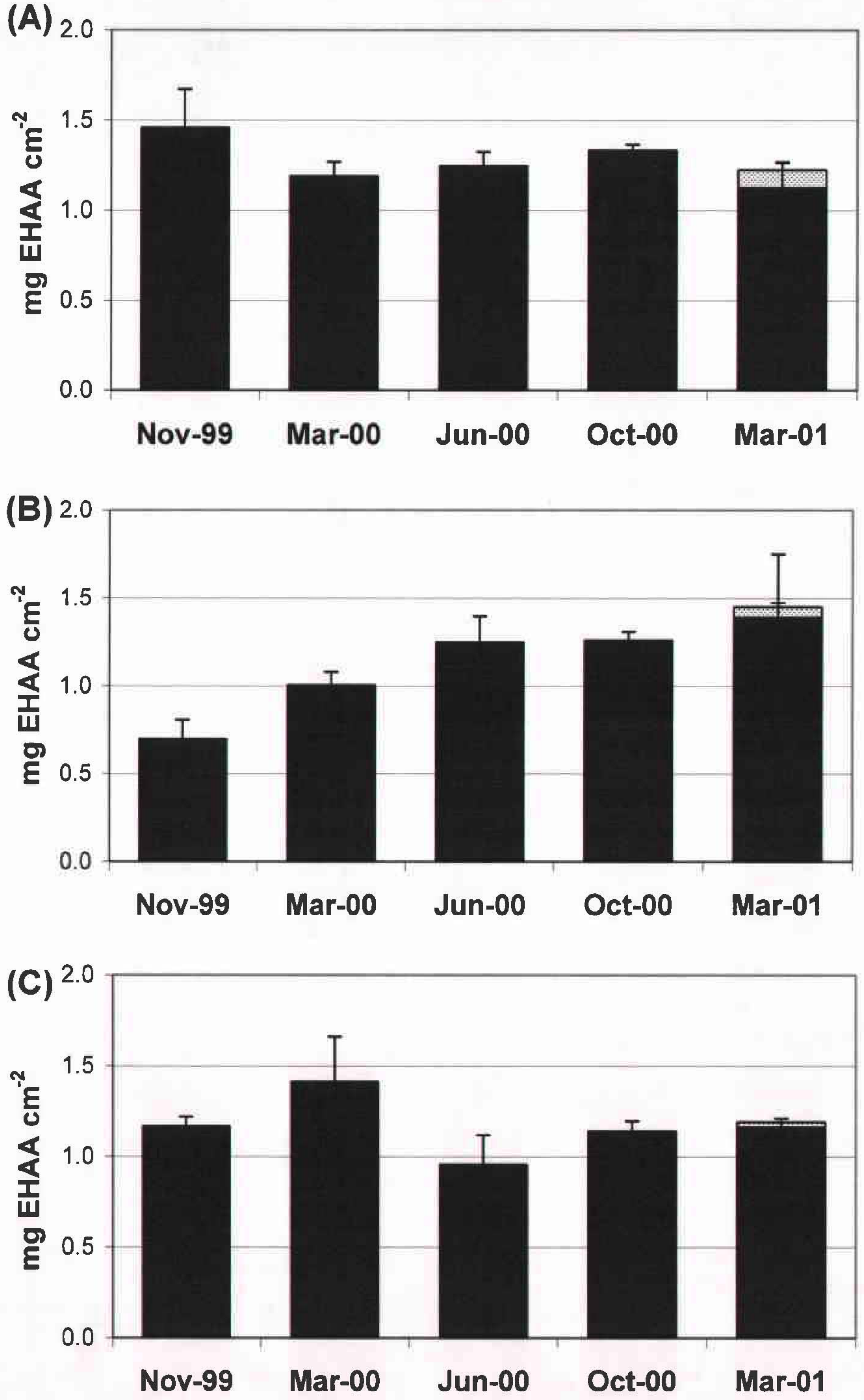


Fig. 7. Inventory of EHAA (mg cm^{-2}) in top 10 cm of sediment at (A) Station A; (B) Station B; (C) Station C. The stippled portion of the Mar-01 bar in each figure represents the mg EHAA cm^{-2} in the phytodetrital layer. N = 3 to 5 cores per time point. Error bars are ± 1 standard error.

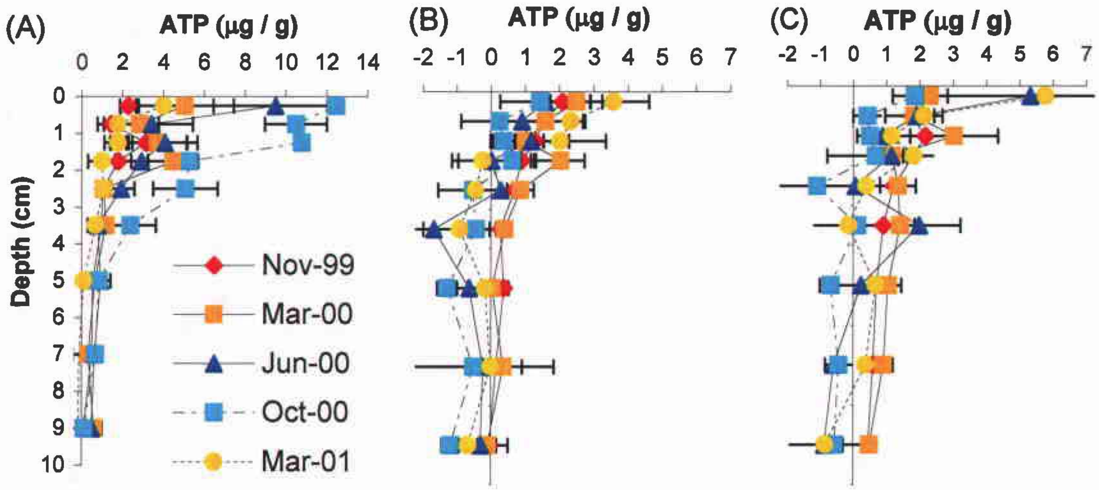


Fig. 8. Sediment ATP concentration (µg ATP g^{-1} sediment dry weight) in top 10 cm at (A) Station A; (B) Station B; (C) Station C. Note the different scales between (A) and (B) and (C). Note the difference in scale between Fig. (A) and Figs. (B) and (C). Each profile represents mean concentration (N = 4 to 5). Error bars are ± 1 standard error.

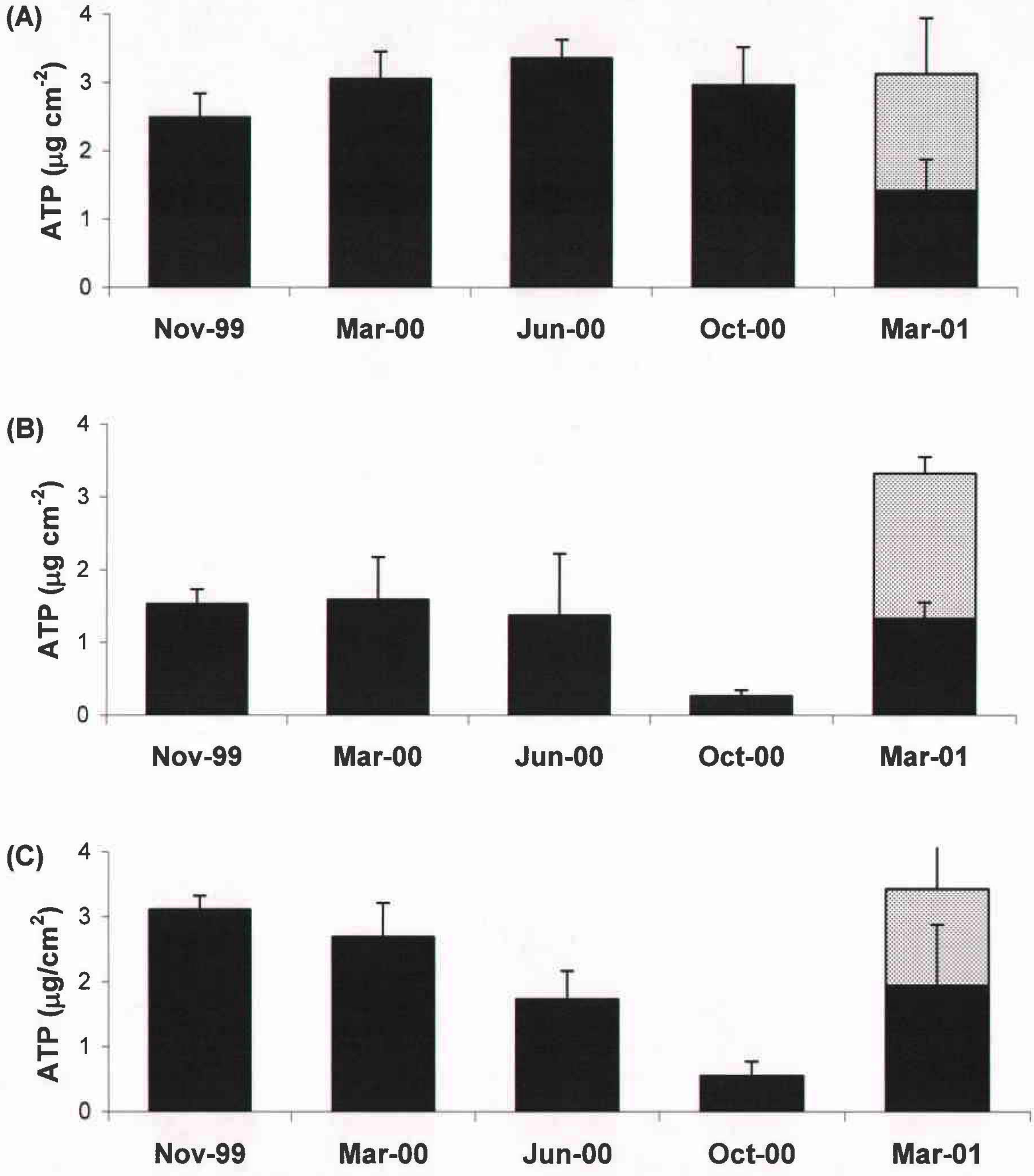


Fig. 9. Inventory of ATP (µg ATP cm^{-2}) in top 10 cm at (A) Station A; (B) Station B; (C) Station C. The stippled portion of the Mar-01 bar in each figure represents the mg ATP cm^{-2} in the phytodetrital layer. N = 4 to 5 cores per time point. Error bars are ± 1 standard error.

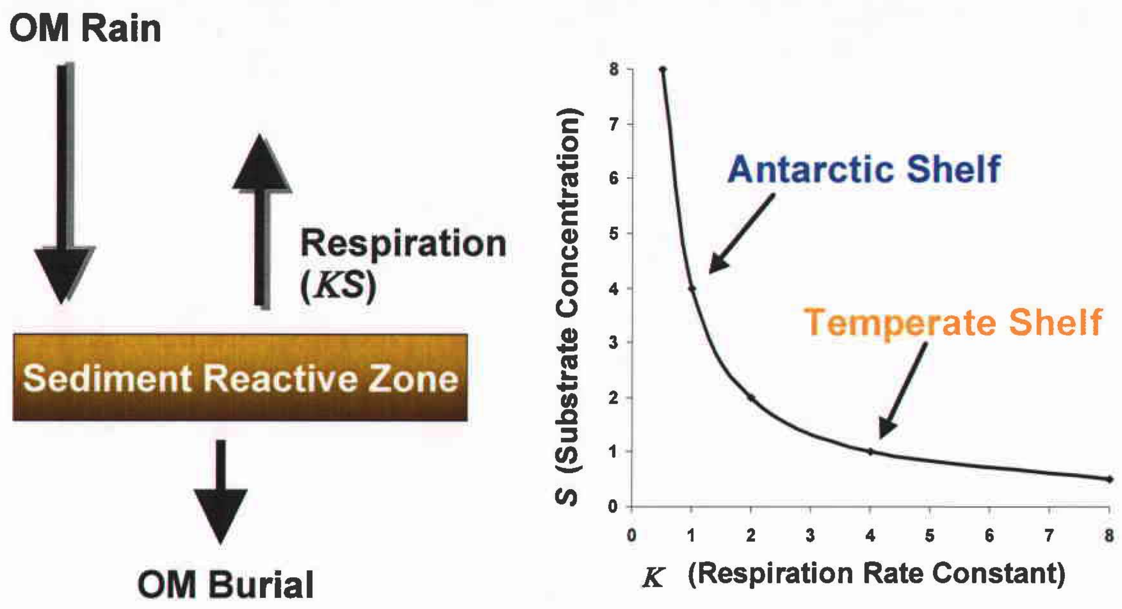


Fig. 10. Conceptual relationship between substrate concentration (S) and degradation rate (κ) in sediments. The line indicates constant respiration, which is a function of S and κ. Antarctic sediments (permanently cold, high substrate) function at high S, low κ, whereas temperate sediments (moderate temperature, low substrate) function at low S, high κ. Each system can thus maintain an equivalent respiration rate via different mechanisms.

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CHAPTER 3. TROPHIC RELATIONSHIPS AMONG BENTHIC MEGAFAUNA ON THE WEST ANTARCTIC PENINSULA SHELF: A STABLE ISOTOPES APPROACH

ABSTRACT

Summer bloom-derived phytodetritus settles rapidly to the seafloor on the West Antarctic Peninsula (WAP) continental shelf, where it appears to degrade relatively slowly, forming a sediment "food bank" for benthic detritivores. Here we use stable carbon and nitrogen isotopes to examine sources and sinks of particulate organic material reaching the WAP shelf benthos (550-650 m depths), and to establish trophic linkages among the most abundant benthic megafauna. We measured $\delta^{13}C$ and $\delta^{15}N$ values in major megafaunal and macrofaunal taxa ($n = 26$) and potential food sources, including suspended and sinking particulate organic matter, ice algae, sedimentary organic carbon, phytodetritus, and macrofaunal polychaetes. The broad (>14‰) range in $\delta^{13}C$ values of the plankton was narrowed considerably in sediments, where little seasonal or interannual variability in stable isotope signatures were observed. Nonetheless, we also measured a broad range of $\delta^{13}C$ values in benthic megafauna, indicating a variety of trophic types. One group of organisms, largely containing deposit feeders, appeared to rely on fresh detritus recovered from the sediments, and sediment organic material that had been reworked by sediment microbes. A second group of animals, including many mobile invertebrate and fish predators, appeared to utilize epibenthic or pelagic food resources such as zooplankton. One surface deposit-feeding holothurian (*Protelpidia murrayi*) exhibited seasonal variability in stable isotope values of body tissue, while other deposit-feeders showed no evidence of seasonal variability in food source or trophic position.

Bloom-derived detritus appears to be the primary source of organic material supplied to the detritivorous benthos; however, seasonal variability in the supply of this material is not mirrored in the sediments, and only to a minor degree in the benthic fauna. This pattern suggests substantial inertia in benthic-pelagic coupling, whereby the sediment ecosystem integrates long-term variability in production processes in the water column above.

INTRODUCTION

The West Antarctic Peninsula (WAP) shelf is subject to highly seasonal deposition of particulate organic carbon (POC) (see Karl *et al.*, 1996) derived from large summer phytoplankton blooms in December-March, following the retreat of winter sea ice (e.g., Smith *et al.*, 1996). These blooms are comprised of both ice algae released from melting sea ice and pelagic phytoplankton released from light-limitation as the ice edge retreats. Sediment-trap data from the Antarctic continental shelf indicate that annual particle fluxes in the near-shore environment are orders of magnitude larger during summer than in ice-covered winter months (Wefer *et al.*, 1988; Dunbar *et al.*, 1989; Honjo, 1990). Furthermore, rapid production of POC during the summer bloom may result in a large proportion of the new production in coastal waters reaching the seabed (Smith *et al.*, in prep.; Honjo, 1990; Karl *et al.*, 1996; Nelson *et al.*, 1996).

Summer pulses of phytodetritus likely represent the primary input of organic material to benthic communities on the WAP shelf (Smith *et al.*, in prep.). Such seasonal phytodetrital pulses are known to induce temporal variability in benthic ecological processes and carbon cycling in other regions (e.g., Grebmeier *et al.*, 1988; Grebmeier and McRoy, 1989; Gooday and Turley, 1990; Ambrose and Renaud, 1995; Pfannkuche *et al.*, 1999; Beaulieu, 2002). Nonetheless, in WAP shelf sediments food availability is likely to exhibit much less seasonality than in the water column (Gutt, 2000; Mincks *et al.*, 2005), because WAP shelf sediments appear to store labile organic material on time scales of months to years, forming a persistent sediment "food bank" for benthic detritivores (Chapter 2; Mincks *et al.*, 2005).

Abundance and biomass of benthic organisms on the Antarctic continental shelf and slope are typically high compared to other shelf and deep-sea environments (reviewed in Arntz *et al.*, 1994; Glover *et al.*, 2005). Thus, detritivore feeding on bloom-derived material could have a large impact on the quantity and quality of organic material ultimately buried in the sediments. Feeding activities and trophic relationships of benthic fauna must be evaluated to determine the fate of bloom material reaching the sea floor. Studies of food web structure, which historically relied on gut-content analyses, are increasingly employing stable isotope techniques (e.g., Hobson and Welch, 1992; Iken *et al.*, 2001). However, very few such studies have been performed in Antarctic ecosystems, particularly for benthic communities (but see Kaehler *et al.*, 2000; Dunton, 2001; Nyssen *et al.*, 2002).

The stable isotopic signature of an organism's tissues is generally related to that of its food source, such that the heavy isotopes of carbon (^{13}C) and nitrogen (^{15}N) undergo a stepwise enrichment between food source and consumer tissues (reviewed in Michener and Schell, 1994). On average, consumers are enriched relative to food material by about 3-5‰ in $\delta^{15}N$, and by <1‰ in $\delta^{13}C$ (DeNiro and Epstein, 1981;

Minagawa and Wada, 1984; Peterson and Fry, 1987). The smaller fractionation of $\delta^{13}C$ makes it useful in distinguishing between food sources with distinctly different $\delta^{13}C$ signatures, whereas $\delta^{15}N$ is better suited to delineating trophic levels (e.g., Peterson and Fry, 1987; Hobson and Welch, 1992). The ratios of stable C and N isotopes ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) are thus useful in determining an organism's trophic position within a community, as well as the sources of organic material sustaining that community. Stable isotope analysis is particularly useful for trophic studies of deposit-feeders, in which sources of ingested organic material are difficult to identify visually (e.g., Hentschel, 1998). Further, since stable isotope analysis measures material incorporated into an organism's tissues, it provides a time-averaged indication of material actually assimilated by the organism, rather than a snapshot of the material consumed at a particular point in time and space.

In this study, we used stable isotope methods to examine sources and sinks of particulate organic carbon reaching the WAP shelf benthos. Our objectives were to (1) identify the primary source(s) of particulate organic flux to the WAP shelf (e.g., ice algae, free-living phytoplankton), (2) determine the relative contribution of these primary sources to the mega- and macrobenthic food web, and (3) elucidate trophic linkages among the most abundant mega- and macrobenthos. Recent evidence of a sizeable detritivore "food bank" persisting in sediments throughout low-flux winter months (Mincks *et al.*, 2005), led us to predict little seasonal change in stable isotope values of the benthos, despite extreme annual/interannual variability in particulate organic-carbon flux. Such dampening of seasonal variability in sediments was expected to yield relatively weak bentho-pelagic coupling on seasonal time scales.

MATERIALS AND METHODS

As part of the FOODBANCS program (see Chapter 2) samples were collected on a series of five cruises to the West Antarctic Peninsula (WAP) continental shelf. These cruises were conducted over a 17-month period encompassing two summer bloom seasons, occurring in (I) Nov/Dec 1999 (early summer-bloom season), (II) Mar 2000 (end of the summer bloom), (III) Jun 2000 (winter oligotrophic period), (IV) Oct 2000 (end of winter, during winter sea-ice retreat) and (V) Feb-Mar 2001 (second summer bloom) (Fig. 2.2). Three stations (A, B, and C) were sampled along a northwest to southeast transect across the continental shelf near Anvers Island (Fig. 1). Water depth was 500-650 m at all stations sampled for this study (Table 1.1). Sonar and photographic surveys (C. Smith *et al.*, unpublished data) revealed little topographic relief at Stations B and C. However, Station A was located in a basin approximately 25 km wide, so topographic focusing could have influenced sediment processes in this area.

Field methods

Surface plankton samples were collected using a 12" ring net (20 μm mesh), which was towed by hand behind the ship as it idled forward (~2 knots) for up to 80 minutes. Oblique plankton tows were also conducted from the surface to within 20-50 m of the seafloor using a Tucker Trawl with three 1-m^2 opening-closing nets (80 μm mesh). Plankton samples used for stable isotope analysis were frozen in bulk, without removal of zooplankton. Additional plankton samples were preserved in 10% formalin for microscopic analysis. Ice algae were harvested on cruise I (Nov 99) and cruise IV (Oct 00) by lowering a 5-gallon bucket over the side of the ship to collect several pieces of sea ice (~15 to 40 cm diameter). Ice fragments were allowed to melt in plastic bags, and particulate material that settled out of the melt water was collected and freeze-dried.

Two replicate, single-cup sediment traps (cf., Dunbar *et al.*, 1989) with effective mouth openings of 0.159 m^2 were deployed on a single mooring at 150 and 170 m above bottom, in the vicinity of Station B (Fig. 1). Traps were deployed on the first cruise in Nov 99, and contents were recovered on each of the four subsequent cruises (i.e., at 90 to 120 d intervals) until the final recovery in Mar 01. Collecting cups on each trap were filled with hypersaline formalin solution (5% NaCl wt/wt, 10% formalin vol/vol) before deployment, and swimmers such as pelagic copepods were removed from samples after recovery using a dissecting microscope. Aliquots of trap samples were freeze-dried prior to stable-isotope analysis.

Sediment tube cores (10-cm diameter) were collected on every cruise, from each of at least five randomly located deployments per station, using a Bowers & Connelly Megacorer. Overlying water was siphoned off, and the cores were sliced into discrete layers down to 10 cm. Surface (0-0.5 cm) and subsurface (4-6 cm) layers of sediment were frozen in individual plastic bags. When a phytodetrital layer (greenish flocculent material with fecal pellets and intact phytoplankton cells) was visible at the surface of a core (Cruise V only), it was suctioned off with a plastic syringe, and stored for separate analysis. Sediments and phytodetritus were stored at -20°C, and freeze-dried prior to analysis.

Additional tube cores were also collected for macrofaunal analyses, and preserved in 10% formalin. These samples were washed on a 300 μm sieve, and sorted under a dissecting microscope. Formalin preservation can have moderate effects on stable isotope signatures. We performed tests of the effect of preservation on stable isotope values using frozen and formalin-preserved animal tissues. These tests yielded only small, statistically insignificant differences in $\delta^{13}C$ or $\delta^{15}N$ between preservation methods (R. Jeffreys *et al.*, unpublished data). Other authors also report small (1‰) decreases in $\delta^{13}C$ with formalin preservation (Rau *et al.*, 1982; Bosley and Wainright, 1999; Kaehler and Pakhomov, 2001), and between 0 and 1.4‰ increases in $\delta^{15}N$ (Bosley and Wainright, 1999; Kaehler and Pakhomov, 2001).

Benthic megafauna were collected using a 5.5 m semi-balloon otter trawl with 2 cm mesh ($n = 1$ to 3 trawls per station on each cruise). Trawl contents were rinsed with raw seawater, and hand-sorted into major taxonomic groups. The most abundant taxa were selected as target organisms for stable isotope analysis. Up to 10 individuals of each taxon were individually flash-frozen in liquid N_2, and stored at -20 or -80°C prior to analysis. Representative specimens were also preserved in 10% formalin and filtered seawater for taxonomic identification.

Stable isotope analysis

The most abundant infaunal, epibenthic, and demersal megafauna were selected for inclusion in the food web analysis. In addition, infaunal spionid polychaetes (*Aurospio* sp. n.; sieve size >300 μm) were chosen from the macrofauna, which was dominated by polychaetes, to represent potential infaunal prey items for larger invertebrates and/or fishes. These taxa represent eight phyla, and a variety of trophic groups, including suspension-feeders, surface and subsurface deposit-feeders, and predators/scavengers.

Frozen megafaunal invertebrate samples were defrosted and dissected to obtain appropriate tissues. Wherever possible, we analyzed body wall or muscle tissue; however, to obtain adequate tissue masses for analyses, we used whole asteroid arm pieces, whole pycnogonid legs, ligament from the Aristotle's lantern of the regular echinoids, and gonad from the irregular echinoids. Due to their small size, macrofaunal polychaetes (*Aurospio* sp.) were analyzed whole, with 10 to 15 individuals pooled together for each measurement.

Animal tissues and some sediment samples were dried in a drying oven at 60°C. Plankton, ice algae, sediment trap material and additional sediments were freeze-dried. Calcareous animal tissues (e.g., asteroid arm pieces), plankton, sediment, and sediment trap samples were acidified with either 6% H_2SO_4 or 10% HCl (cf., McConnaughey and McRoy, 1979; Hobson and Welch, 1992) to remove carbonates. Dried samples were ground and homogenized, and subsamples measured into tin boats for analysis.

All stable isotope analyses were performed at the University of Hawai'i at Manoa, SOEST mass spectrometer facility. Samples were loaded in an autosampler and analyzed on a Carla Erba NC2500 elemental analyzer. Samples were dropped into a vertical quartz tube and flash-combusted in pure oxygen at 1020°C. N_2 and CO_2 were then introduced into a Finnigan DeltaS ion ratio-monitoring mass spectrometer in dual-elemental mode via a Finnigan ConFloII interface. Isotope ratios are expressed as parts per thousand (‰) differences from standard reference material according to the following equation:

$$\Delta X = [(R_{\text{sample}} / R_{\text{standard}}) - 1] \times 1000$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. $R_{standard}$ for ^{13}C and ^{15}N are from PeeDee Belemnite (PDB) and atmospheric N_2, respectively. A reference material, cicloesanone, was analyzed approximately every eight samples, indicating analytical errors of ± 0.12 and 0.2‰ for C and N, respectively.

Statistical analyses were conducted with the Statistical Package for the Social Sciences (SPSS) software package, and an alpha level of 0.05 was used as the criterion of statistical significance.

RESULTS

Plankton and sedimenting particulate organic matter (POM)

Net-collected plankton included both large algal cells (particularly diatoms) and zooplankton. Stable isotope analyses were performed on the bulk plankton samples, so seasonal differences in isotopic composition of the plankton may reflect changes in zooplankton abundance (especially krill larvae and juveniles), as well as seasonal variations in phytoplankton. Microscopic examination of fresh and formalin-preserved plankton samples indicated very low abundance of large phytoplankton in Nov 99. In Mar 00, the centric diatom *Corethron criophilum* was very abundant in plankton samples. Winter net tows (Jun 00) were composed mainly of juvenile krill and salps. The following spring (Oct 00), *C. criophilum* was again abundant in plankton samples from all stations. By summer (Mar 01), a different suite of diatoms had appeared, with *Coscinodiscus* cf. *bouvet* dominating at Station A, *Rhizosolenia* spp. dominating at Station C, and a mixture of both types occurring at Station B.

Seasonal and interannual changes in $\delta^{13}C$ were evident in net-collected plankton (multivariate ANOVA, F = 2.596, $p = 0.095$), whereas $\delta^{15}N$ did not vary significantly throughout the sampling period (Fig. 2). This variability in stable isotopic signature coincides with the changes in the dominant species of pelagic diatom collected each season, as well as seasonal variations in the relative abundances of zooplankton and phytoplankton, highlighting the temporal variability in plankton community dynamics. The interannual differences in the plankton overshadowed seasonal differences. Based on *post hoc* comparisons (Least Significant Difference), there were no seasonal changes in plankton $\delta^{13}C$ in the1999/2000 bloom season, although we did detect significant differences between spring (Oct) and summer (Mar) in 2000/2001 ($p = 0.052$). However, the interannual differences between summer 2000 and summer 2001 ($p = 0.029$) were more substantial. Much of the temporal variability in plankton $\delta^{13}C$ occurred at Stations A and B, with values ranging from –15 to –33‰, and –18 to –31‰, respectively (Table 1). Maximum values at these stations in Mar 01 were similar to ice algae, whereas plankton from Station C (Oct 00-Mar 01) was more similar to pelagic diatoms, at about -26 to -30‰.

Multivariate ANOVA indicated significant seasonal variability in both $\delta^{13}C$ and $\delta^{15}N$ of sedimented particulate material in traps (F = 32.922; $p = 0.003$ and F = 9.659; $p = 0.026$, respectively); however, the range in isotopic values was much narrower for trap material than for net plankton (Fig. 3). The $\delta^{13}C$ values of sediment trap material collected in Nov 99-Mar 00 and Mar 00-Jun 00 resembled that of net plankton from Mar 00 (Fig. 2), suggesting that the bulk of material in the traps was deposited during the summer phytoplankton bloom. In addition, sediment trap material from this period was depleted in $\delta^{15}N$ (~2.5‰), indicating relatively fresh algal material. The average $\delta^{13}C$ values of material in these traps (~ -30‰) indicates pelagic diatoms, rather than ice algae (-19‰), were the most likely source of sinking particulate organic material.

The $\delta^{13}C$ values of particulate matter trapped in winter (Jun 00-Oct 00) matched net plankton from the beginning and end of this period. The $\delta^{15}N$ value of the Jun 00–Oct 00 trap material was only enriched by about 1‰ relative to plankton, but about 3.5‰ more enriched than trap material collected in other months. $\delta^{15}N$ enrichment during winter months suggests settling of more degraded material such as krill fecal strings and exuviae, following the cessation of the summer bloom.

Sediment-trap material collected during the second summer bloom period (Oct 00-Mar 01) was >2‰ enriched in $\delta^{13}C$ than the previous year, but similar in $\delta^{15}N$ (Fig. 2). However, $\delta^{13}C$ values of plankton at Station B (where traps were deployed) varied more than 10‰ between years. The large input of material that had reached sediment traps by Mar 01 was also comprised of different diatoms than were present in the overlying surface waters at that time. Under microscopic examination, sediment trap material recovered in Mar 01 was found to contain abundant and relatively intact cells of *Corethron criophilum*, whereas Mar 01 plankton tows were dominated by *Coscinodiscus* sp. and *Rhizosolenia* sp.

Sediments and phytodetritus

The range in $\delta^{13}C$ values narrowed between plankton and sediment trap samples, and narrowed slightly further still between sediment traps and surface sediments (Fig. 3). In general, surface sediments were slightly enriched in both ^{13}C and ^{15}N relative to sediment trap material, indicating dilution by a pool of more refractory material at the seafloor and/or additional transformation of organic material in the water column below trap depths. Surface sediments at Station A were significantly more enriched in $\delta^{13}C$ (2‰) than those at the other stations (One-way ANOVA; F = 6.437, p = 0.013) (Fig. 4). However, there were no significant temporal changes in $\delta^{13}C$ at Station A. $\delta^{15}N$ values, in contrast, did vary temporally (F = 11.593, p = 0.010), with depleted values in Oct 00, and greater enrichment in Mar 01 than in other months. $\delta^{13}C$ and $\delta^{15}N$ values did not vary significantly across time at Station B or C (note no data for Jun 00 and Oct 00 at Station B).

Subsurface sediments (4-6 cm depth) were only analyzed from the two summer sampling periods (Mar 00 and Mar 01), and did not vary significantly between years in either $\delta^{13}C$ or $\delta^{15}N$ at any of the stations. $\delta^{13}C$ values of subsurface sediments roughly matched those of surface sediment at all stations (Fig. 4). $\delta^{15}N$ values were enriched in subsurface relative to surface sediments by 0-4‰ at all stations.

The $\delta^{13}C$ values of phytodetritus (Mar 01 only) fell mid-way between values for plankton in Oct 00 and Mar 01, indicating derivation from summer phytoplankton-bloom material. A $\delta^{15}N$ enrichment in phytodetritus relative to plankton was only observed at the more northerly Station C, where ice-cover is likely to have disappeared first, and bloom material to have settled out earlier in the season. At Station A, phytodetritus matched surface sediments in $\delta^{15}N$, but was 1‰ enriched in $\delta^{13}C$. In contrast, Station B and C phytodetritus was 1-2‰ enriched in $\delta^{15}N$, but equivalent to surface sediment in $\delta^{13}C$ value.

Benthic fauna

Mean stable isotope values for all taxa are summarized in Table 2 and Fig. 5. We observed a broad range in $\delta^{13}C$ values, from about -17 to -27‰. In contrast, all but two species fell within a 4‰ range in $\delta^{15}N$. Given typical trophic-level enrichments (or "trophic shifts") of about 3.5‰ for $\delta^{15}N$ and 1‰ for $\delta^{13}C$ (e.g., Rau *et al.*, 1983; Michener and Schell, 1994), the small range in $\delta^{15}N$ values measured here suggests that most of the sampled animals, including predatory fish and octopus, occupy approximately two trophic levels. Based on these trophic shift assumptions, a standard predatory food chain should have a slope of ~3.5 on a plot of $\delta^{13}C$ vs. $\delta^{15}N$. The slope of the $\delta^{13}C$ vs. $\delta^{15}N$ relationship in our study is much lower, with mobile demersal predators (fish and octopus) falling along a line with a slope of ~1.5 (Fig. 6). Surface and subsurface deposit-feeders lie along separate trend lines with even lower slopes (~0.27). Invertebrate predators and scavengers are very broadly distributed in $\delta^{13}C$ and $\delta^{15}N$ space. Two organisms, the sponge *Cinachyra antarctica* and the pencil urchin *Ctenocidaris perrieri*, exhibited unusually enriched $\delta^{15}N$ values, but fell within the same $\delta^{13}C$ range as the other organisms.

To identify potential food sources, trophic-shift boxes enclosing the expected ranges of enrichment in $\delta^{13}C$ and $\delta^{15}N$ (0-1‰ and 3-5‰, respectively) from feeding on a particular food source are plotted in Fig. 7. Surface-deposit feeders generally fall into the trophic-shift boxes for "sediment trap material" and "surface sediments", matching our expectations for stable isotope enrichment. In contrast, subsurface deposit feeders fit poorly into the "subsurface sediments" box, exhibiting a wider $\delta^{13}C$ range than expected.

Seasonality in isotopic composition

A few of the most abundant taxa were examined for seasonal patterns in stable isotope signatures, including the surface deposit-feeding holothurians *Peniagone* sp. and *Protelpidia murrayi* (Fig. 8) and polychaetes *Aurospio* sp. n. (Fig. 9), the bivalve *Limopsis marionensis* (Fig. 10), and the suspension-feeding crinoid *Promachocrinus kerguelensis* (Fig. 11). Seasonal differences for each taxon were tested using multivariate ANOVA, with Least Significant Difference (LSD) *post-hoc* comparisons used to resolve individual interactions between time points. Significant temporal variability was detected only in the two surface deposit-feeding holothurians, and in the crinoid.

In *Peniagone* sp., multivariate ANOVA indicated significant temporal variation in $\delta^{15}N$ (F = 5.224, $p = 0.014$), with no significant differences in $\delta^{13}C$. *Post hoc* comparisons for $\delta^{15}N$ revealed significant differences between Mar 01 and all other time points sampled (Table 3). *Protelpidia murrayi* exhibited much more temporal variability in stable isotope ratios than *Peniagone* sp. (Fig. 8), with significant differences in both $\delta^{13}C$ (F = 7.199, $p = 0.006$) and $\delta^{15}N$ (F = 10.576, $p = 0.001$). Results of *post hoc* comparisons (Table 3) indicate differences in $\delta^{13}C$ between Nov 99, and both Mar 00 and Jun 00, as well as an interannual difference between Mar 00 and Mar 01. $\delta^{15}N$ varied seasonally between Nov 99 and Mar 00, and interannually between summer 1999/2000 and summer 2000/2001.

Promachocrinus kerguelensis (Fig. 11) varied significantly across time in $\delta^{15}N$ (F = 7.757, $p = 0.009$); however, the 2‰ variation in $\delta^{13}C$ was only statistically significant at an alpha level of 0.10 (F = 3.439, $p = 0.072$). $\delta^{15}N$ varied significantly between winter and spring (Jun and Oct), and between winter and summer (Jun and Mar) in the 2000/2001 bloom season (Table 3).

DISCUSSION

Results of stable isotope analyses suggest that the bulk of sedimenting organic material on the WAP shelf is derived from the summer phytoplankton bloom. This material appears to arrive with relatively minimal degradation at the seafloor. While substantial seasonal and interannual variability occurred in the stable isotope signature of net-collected plankton, this variability was observed to a lesser degree in sediment traps, and not observed in surface sediments (Fig. 2). Benthic megafauna exhibited a broad range in $\delta^{13}C$ values, but only a narrow range in $\delta^{15}N$ for the majority of taxa, resembling a "trophic continuum" rather than a classic linear food chain. While the spionid polychaetes and the bivalve *Limopsis marionensis* exhibited constant stable isotope signatures year-round, surface deposit-feeding holothurians (especially *Protelpidia murrayi*; Fig. 8) and the suspension-feeding crinoid *Promachocrinus kerguelensis* (Fig. 11) revealed temporally varying stable isotope signatures, likely reflecting a similar seasonal pattern in sedimenting POM. These taxa were substantially (3-6 ‰) enriched in $\delta^{13}C$ relative to trap material and surface sediments, and would appear to be deriving nutrition from these sources. However, given the lack of seasonality in $\delta^{13}C$ values of surface sediments, seasonality in surface deposit-feeders suggests substantial selectivity for components of the freshly deposited POC (i.e., similar to trap material).

Temporal variability in particulate organic material (POM) and sediments

The >10‰ range in stable carbon isotope values of net-collected plankton agrees with the seasonal and interannual variability in summer bloom dynamics evident in other aspects of the FOODBANCS study (e.g., C. Smith *et al.*, in prep.; Mincks *et al.*, 2005). Depleted $\delta^{13}C$ values (< -30‰) detected in spring and summer are representative of Southern Ocean phytoplankton communities, which are typically depleted to similarly low levels (e.g., Wada *et al.*, 1987; Fischer, 1991; Rau *et al.*, 1991b; Nyssen *et al.*, 2002). Slow, light-limited growth of Antarctic phytoplankton in the presence of high $CO_{2(aq)}$ concentrations is thought to promote strong carbon fractionation, yielding unusually large $\delta^{13}C$-depletion in phytoplankton and derived POM (e.g., Fry and Sherr, 1984; Wada *et al.*, 1987; Fischer, 1991; Rau *et al.*, 1991b). Both stable isotope data and qualitative microscopic observations of plankton samples indicate springtime abundance of the diatom *Corethron criophilum* in the 1999/2000-bloom season, followed by late summer/early winter increases in juvenile krill densities (Wada *et al.*, 1987; Fischer, 1991; Frazer, 1996). We observed a similar abundance of *C. criophilum* in the plankton the following spring (Oct 00), although the magnitude of the subsequent summer bloom in early 2001 was much greater than in the previous year (Mincks *et al.*, 2005; C. Smith *et al.*, in prep.).

$\delta^{13}C$ values of plankton samples from the two summer seasons were markedly different (10‰; Fig. 2), with the most dramatic difference at Station A (Table 1). This interannual increase in $\delta^{13}C$ coincided with a change in the assemblage of diatoms from the *C. criophilum*-dominated community at all stations in Oct 00. In Mar 01, we observed a gradient across the shelf, with a community dominated by *Coscinodiscus* sp.

at Station A, to a *Rhizosolenia*-dominated community at Station C. $\delta^{13}C$ enrichments on the order of 10‰ reported elsewhere in Antarctic waters were accompanied by both a change in the diatom assemblage and a large increase in primary production (Fischer, 1991; Dunbar, 1992; Deharis *et al.*, 1997). According to these studies, high levels of primary production may affect carbon fractionation due to differences in carbon demand between fast- and slow-growing phytoplankton assemblages (i.e., high-productivity waters may become CO_2-limited). ^{13}C-enrichment is also common during the spring blooms typical of many other coastal areas (e.g., Fry and Wainright, 1991; Nakatsuka *et al.*, 1992; Canuel *et al.*, 1995). Thus, $\delta^{13}C$ enrichment in Mar 01 plankton was likely related to a dramatic increase in primary productivity during the ice edge-associated summer bloom formation. While $\delta^{13}C$ enrichment is also common in ice algae due to biologically driven $CO_{2(aq)}$ depletion within sea-ice (Wada *et al.*, 1987; Hobson *et al.*, 1995; Gibson *et al.*, 1999), we do not believe ice algae made a significant contribution to the high $\delta^{13}C$ signatures found in our net plankton in late summer 2001. Sea ice had been absent at all our stations for 2-3 months prior to our Mar 01 sampling (Fetterer and Knowles, 2004), and the relatively large mesh size (80 μm) used for most of our plankton tows should have missed many abundant ice-associated nanoplankton such as *Phaeocystis* spp. (e.g., El-Sayed and Fryxell, 1993).

The broad range in $\delta^{13}C$ values in the plankton was not observed in sediment traps (Figs. 2 & 3), presumably because the bulk of material reaching the traps deposited during summer months, and should have consisted mainly of bloom-forming diatom detritus and fecal pellets. POM collected in our traps during summer 2000/2001 (Oct 00-Mar 01) appeared, under microscopic examination, to consist largely of the diatom

Corethron criophilum. Further, trap material had nearly the same $\delta^{13}C$ signature as net plankton from Oct 00 (~ –28‰), which also contained abundant *C. criophilum*. Sinking fluxes of this diatom in ice-edge habitats are known to produce $\delta^{13}C$ values equivalent to those reported here for sediment traps and plankton (Bathmann *et al.*, 1991), whereas $\delta^{13}C$ of sedimenting ice algae and krill fecal pellet strings released upon the initial break-up of winter sea ice typically measure -20 to -25‰ (Wada *et al.*, 1987; Fischer, 1991; Frazer, 1996). Thus, ice algae did not appear to contribute significantly to sinking POM during the high-flux summer months in our study area. In addition to the apparent lack of ice algae, the Oct 00 – Mar 01 traps also contained different diatoms (i.e., *C. criophilum*) than those found in the dense phytoplankton bloom underway in Mar 01 (*Coscinodiscus* and *Rhizoloenia* spp.). The initial large spring/summer flux event of *C. criophilum* thus appears to have given way to a secondary bloom that was substantially later in the summer than the bloom of 1999/2000. Consequently, organic particle flux to the benthos may have continued later into the fall and winter in 2001 than in 2000.

The $\delta^{15}N$ depletion of sediment trap material, particularly between Nov 99 and Mar 00 (Fig. 2), suggest that relatively undegraded algal material was captured in the traps. Sedimentation of fresh algal material to within 150 m of the seabed points to rapid sinking of bloom material during this period, such that minimal degradation could have occurred in the water column. This rapid sinking should have resulted in the delivery of a highly labile food source for the benthos. Indeed, surface sediments and phytodetritus showed little additional ^{15}N-enrichment relative to traps at 150 m above bottom, particularly at Station A (Table 1, Fig. 2). At Station C, Mar 01 net plankton was substantially more depleted in $\delta^{15}N$ than the phytodetritus and surface sediments directly below. However, phytodetritus at the more northerly Station C was likely deposited from ice-edge blooms earlier in the season (Fetterer and Knowles, 2004), which had subsequently been replaced by the open-water phytoplankton assemblage (i.e., *Rhizosolenia* spp.) collected in plankton nets in Mar 01.

The presence of a thick phytodetrital carpet in Mar 01, which was not observed in the previous summer, provides further evidence of large interannual variability in particle flux on the WAP shelf. $\delta^{13}C$ values of phytodetritus were enriched relative to sediment-trap material (Fig. 2), suggesting degradation of phytodetrital material at the seafloor and/or dilution with more refractory sedimentary organic carbon. Dilution seems more likely, because the high concentrations of Chl-*a* in phytodetritus (Mincks *et al.*, 2005) indicated the presence of substantial fresh algal material. The $\delta^{13}C$ enrichment of phytodetritus could also reflect, in part, colonization by bacteria and meiofauna from the sediment surface (e.g., Rau *et al.*, 1983). $\delta^{13}C$ enrichments at the sediment-water boundary, ranging from 1‰ up to 3-4‰, have been reported elsewhere on the Antarctic continental shelf, and are attributed to varying intensity and/or mode of benthic remineralization (Fischer, 1991).

Trophic relationships among benthic fauna

The megabenthic taxa studied here were representative of soft-sediment habitats at comparable depths elsewhere on the Antarctic shelf, which are typically dominated in abundance by polychaetes, molluscs, and crustaceans, and in biomass by echinoderms (e.g., Lowry, 1975; Mühlenhardt-Siegel, 1988; Arnaud *et al.*, 1998; Starmans *et al.*, 1999; Gutt, 2000). Such assemblages are found in relatively quiescent shelf regions with low current velocities, as indicated by the presence of phytodetrital layers at the sediment surface (e.g., Starmans *et al.*, 1999; Beaulieu, 2002). In contrast, shallower, hard-bottom habitats, including large areas of the Weddell Sea, harbor dense assemblages of suspension-feeders dependent on settling and resuspended material carried in strong bottom currents (e.g., Gutt, 1991; Starmans *et al.*, 1999; Orejas *et al.*, 2000; Smith *et al.*, 2005).

The broad range in $\delta^{13}C$ values among WAP shelf benthos (Fig. 5) suggests a variety of feeding strategies and overlapping detrital food resources. Wide ranges in $\delta^{13}C$ values among detritivorous benthos were also reported for a Weddell Sea benthic community (Nyssen *et al.*, 2002) and a seasonally ice-covered community in the high Arctic (Hobson, 1992; Hobson *et al.*, 1995, 2002). Overlapping ranges in stable isotope values can make trophic levels difficult to distinguish, yet this technique proved useful in exploring trophic interactions of WAP shelf benthos, and the importance of bloom-derived detritus in their diet.

Surface deposit-feeders (SDFs) had the narrowest range in isotope values in any of the trophic groups sampled. The holothurians *Peniagone* sp. and *Protelpidia murrayi*, as well as spionid polychaetes (*Aurospio* sp. n.), were sufficiently enriched in ^{13}C and ^{15}N to suggest one trophic level above surface sediments (cf., Michener and Schell, 1994) (Figs. 8 and 9). Synallactid holothurians fell in the same range in $\delta^{13}C$, but were 2‰ more enriched in $\delta^{15}N$. They may be less selective for the freshest particles at the sediment surface, or may obtain some material from deeper sediment layers. Echiurians were ~2‰ enriched in both ^{13}C and ^{15}N relative to other SDFs, and may either be feeding on more refractory material, or selecting for a particular fraction of sediment organic matter such as gardened bacteria (cf., Smith *et al.*, 1986; Jumars *et al.*, 1990; Lovvorn *et al.*, 2005). ^{14}C and $^{234}Th_{xs}$ in deposit-feeder gut contents on the WAP shelf indicate highly efficient particle selectivity in *Peniagone* sp. and echiurians, with the greatest selectivity relative to other deposit-feeders occurring in winter (i.e., Jun 00) (McClintic, 2002; Purinton, 2005).

In contrast to SDFs, subsurface deposit-feeders (SSDFs) spanned the maximum range in $\delta^{13}C$, with ^{13}C-depletion in the irregular urchins (*Amphineustes lorioli* and *A. rostratus*), and enrichment in head-down deposit-feeding holothurians (*Molpadia musculus* and *Paracucumis antarctica*). However, our use of irregular urchin gonad tissue probably affected the $\delta^{13}C$ signature in those taxa. Urchin gonads can vary widely in lipid content over the course of the reproductive cycle (e.g. Galley, 2003), and the high C:N ratio in these tissues (Table 2) indicates high lipid content at the time of collection. Further, C:N ratios are negatively correlated with ^{13}C content, particularly in tissues where C:N > 6 (McConnaughey and McRoy, 1979; Wada *et al.*, 1987; Rau *et al.*, 1991a). Model I linear regression indicated a significant negative relationship between $\delta^{13}C$ and C:N for *A. lorioli* and *A. rostratus* ($R^2 = 0.667, p = 0.004$), whereas no relationship existed for the other taxa. Thus, the general body tissues of the irregular urchins may in fact be more enriched in ^{13}C than indicated here. Body wall $\delta^{13}C$ values for irregular urchins from this area reported by Purinton (2005) ranged from –24 to -10‰, placing them nearer the range of values we measured for the other SSDFs (~-22 to -18‰). SSDF holothurians were ~6‰ more enriched in $\delta^{13}C$ than subsurface sediments (Fig. 5). All the SSDFs were confined to a narrow range in $\delta^{15}N$ values approximately one trophic level (3-5 ‰) above subsurface sediments. However, differences in $\delta^{13}C$ clearly suggest utilization of a range of organic materials in sediments (cf., Lovvorn *et al.*, 2005).

Invertebrate predators and scavengers (P/S) were clustered into two groups (Fig. 5). Members of Group I, including low-mobility and/or sessile predators such as gastropods, asteroids, and the anemone *Hormathia lacunifera*, fell within a ~2‰ range in $\delta^{13}C$ and $\delta^{15}N$, and were generally enriched in ^{13}C relative to the other P/S group. This ^{13}C-enrichment has been seen elsewhere in omnivores and detritivores, and is thought to reflect assimilation of recycled detrital carbon along with carbon from fresh tissue (Hobson *et al.*, 2002). These taxa may also feed on small invertebrates, in addition to scavenging for algal detritus or animal remains. However, most of the predators in Group I were < 2‰ more enriched in ^{15}N than macrofaunal polychaetes. Their diets are likely to include a mixture of detritus, animal tissue, and macrofaunal prey items.

Invertebrate P/S Group II, consisting of more mobile taxa such as pycnogonids (*Colossendeis* sp.), isopods (*Natatolana meridionalis*), octopus (*Pareledone* sp.), regular urchins (*Sterechinus antarcticus*), and giant scale worms (*Laetmonice productia*), was similar to the fishes in $\delta^{13}C$ (Fig. 5). However, fish and invertebrate predator-scavengers from this group spanned a much larger range in $\delta^{15}N$, covering at least two trophic levels (Fig. 6). This range in $\delta^{15}N$ for the mobile predators/scavengers (especially fish) constitutes a fairly linear relationship reminiscent of a classic pelagic predatory food chain (e.g., Brooks and Dodson, 1965; Ryther, 1969). The $\delta^{13}C$ depletion combined with the wider range in $\delta^{15}N$, particularly for the mobile epibenthic predators such as fish and octopus, suggests at least partial dependence on pelagic food sources such as zooplankton, which tend to be more depleted in $\delta^{13}C$. Similar separation between pelagic and benthic feeding groups has been observed elsewhere at high latitudes (McConnaughey and McRoy, 1979; Hobson *et al.*, 1995; Hobson *et al.*, 2002), and may be responsible for the 4‰ difference in $\delta^{13}C$ between the two anemones, *Hormathia lacunifera* and *Isosicyonis alba* (Fig. 5).

Isosicyonis alba was exclusively found attached to the shell of the gastropod *Harpovoluta charcoti*. Like the anemone *Hormathia lacunifera*, *Harpovoluta charcoti* differed from *I. alba* in $\delta^{13}C$ by about 4‰. *I. alba*'s stable isotope signature places it roughly in the range that would be predicted for organisms feeding on juvenile krill (see net plankton values for Jun 00, Fig. 2). Thus, *I. alba* and *H. lacunifera* appear to be capitalizing on quite different food sources, with the latter likely deriving food from the detritus-based benthic system. Substantial trophic separation is also evident between *I. alba* and its gastropod host, *H. charcoti*, which may be a predator on benthic detritivores.

Benthic, detritus-based food webs typically undergo greater (4-5‰) enrichment in ^{13}C, relative to available POM, than pelagic consumers, thus creating the separation between benthopelagic and strictly benthic trophic groups described here (McConnaughey and McRoy, 1979; Hobson *et al.*, 1995; Hobson *et al.*, 2002). This enrichment in benthic detritivores has been attributed to assimilation of microbial and/or meiofaunal biomass or byproducts, and the strong carbon fractionation effects of bacterial metabolism (McConnaughey and McRoy, 1979; Hobson *et al.*, 1995; Nyssen *et al.*, 2002; Lovvorn *et al.*, 2005). Indeed, data from the WAP shelf do indicate potential for extensive reprocessing of phytodetritus by foraminifera (Suhr *et al.*, 2003).

Ctenocidaris perrieri, the "pencil urchin," is an anomalous member of the invertebrate P/S group. Cidarid urchins on the Antarctic shelf are reported to feed on other invertebrates, including molluscs, sponges, and hydroids (Jacob *et al.*, 2003), although Galley (2003) reported sediment in *C. perrieri* guts. Biochemical analysis of *C. perrieri* tissues indicated winter periods of starvation (Galley, 2003), and starvation conditions can also produce enriched $\delta^{15}N$ values (Fantle *et al.*, 1999). Alternatively, *C. perrieri* could have a carrion-rich diet. Similar ^{15}N-enrichment has been noted in scavenging amphipods from the Weddell Sea, known to feed on fish and crustacean remains (Nyssen *et al.*, 2002).

Given the dominance of deposit-feeders on the WAP shelf, we collected few suspension-feeders (SF) in sufficient abundance for stable isotopic analyses. The crinoid, *Promachocrinus kerguelensis*, yielded stable isotope values very similar to those of *I. alba* (Fig. 5). Such values again suggest juvenile krill or other small zooplankton as potential food sources, and imply *P. kerguelensis*' inclusion in the water-column based trophic group.

The sponge *Cinachyra antarctica* yielded curious stable isotope values, similar to *Ctenocidaris perrieri* (Fig. 5). *Cinachyra antarctica* displayed slight enrichment in $\delta^{13}C$, comparable to the subsurface deposit-feeders and low-mobility predators, but $\delta^{15}N$ values were the highest recorded in our study. Because this sponge is unlikely to be an apex predator on the WAP shelf, $\delta^{15}N$ enrichment may be related to the indiscriminate filtering of particulate material from the water column, potentially including a variety of material such as bacteria and their exudates (e.g., Iken *et al.*, 2001; Nyssen *et al.*, 2002).

The soft-sediment benthic community on the WAP shelf appears to be composed of two groups of organisms—one group deriving nutrition primarily from sediments or detritus at the seafloor, and one utilizing epibenthic or pelagic food resources such as zooplankton. This pattern has also been observed in the Arctic (Hobson *et al.*, 2002). A number of other similarities can also be drawn between the WAP shelf and seasonally ice-covered areas of the Arctic. Ice algae did not appear to be a substantial source of food for benthos in either system (Hobson *et al.*, 1995). In addition, most organisms sampled here fell between 7 and 11‰ in $\delta^{15}N$ values, suggesting approximately two trophic levels between POM and benthos. Hobson *et al.* (1992, 1995, 2002) also reported a similarly narrow range in $\delta^{15}N$ for Arctic benthos.

Temporal variability in trophic strategy of benthic megafauna

Benthic fauna on the WAP shelf are thought to experience reduced seasonality in food availability relative to pelagic organisms (Gutt, 2000; Smith *et al.*, 2005; Mincks *et al.*, 2005; C. Smith *et al.*, in prep.), as evidenced by the year-round appearance of relatively fresh detrital carbon in deposit-feeder guts (Galley, 2003; Purinton, 2005). Dampened seasonal and interannual changes in stable isotope signatures of sinking particulates and sediments lend additional support to these observations. Thus, even if carbon and nitrogen turn over rapidly in body tissues (cf., Lorrain *et al.*, 2002; Rossi *et al.*, 2004), we would expect benthic detritivores to show relatively little temporal variation in stable isotope signature, despite the pulsed nature of organic inputs to the sediments. Members of both pelagic and benthic-based trophic groups are examined here to determine effects of temporal variability in particulate flux on feeding behavior.

Two surface deposit-feeding holothurians studied here, *Peniagone* sp. and *Protelpidia murrayi*, were usually found with full guts (Galley, 2003), and appeared to be feeding year-round. *Peniagone* sp. is a highly selective feeder, able to find and ingest the freshest material in all seasons, whereas *P. murrayi* utilizes selective *degradation/ assimilation* to derive enhanced nutritional value from less selectively ingested sediments (DeMaster *et al.*, submitted; Purinton, 2005). Both taxa had similar average isotope values (Fig. 5). However, temporal patterns in $\delta^{13}C$ differed between the two species, with *P. murrayi* showing greater seasonal variability in $\delta^{13}C$ (Fig. 8). This variability in *P. murrayi* may be due to seasonal changes in the proportion of surface sediments composed of relatively fresh detritus. In other words, *Peniagone* sp. is able to select and ingest only the highest food-quality particles, even when they are scarce, whereas *P. murrayi* ingests sediment less discriminately, digesting particular sedimentary components, including bacteria and their exudates. Lovvorn *et al.* (2005) proposed selective use of bacteria as an explanation for ^{13}C-enrichments in some detritivores. Interestingly, maximum ^{13}C values in *P. murrayi* occurred in Nov 99 and Mar 01, concurrently with peaks in microbial biomass (Mincks *et al.*, 2005).

In contrast to the holothurians, the macrofaunal spionid polychaete *Aurospio* sp. n. did not exhibit temporal variability over the three seasons sampled (Fig. 9). Smaller organisms tend to equilibrate faster to seasonal changes in diet (e.g., Schmidt *et al.*, 2003), so this species should be particularly appropriate for tracking seasonal changes in the isotopic value of food. However, mean isotope values for spionids were very similar to those for both holothurians described above, suggesting a similar source of food particles for all these surface deposit-feeders. Smaller (macrofaunal) deposit-feeders like

Aurospio sp. n. may be constrained by gut size to utilize greater particle-selectivity than larger organisms, in order to maximize nutritional intake (Jumars *et al.*, 1990). Thus, this species might be expected to exhibit less variability in isotope values compared to holothurians. In any case, food-rich particles appear to be available to particle-selective surface deposit-feeders year-round on the WAP shelf.

Like *Aurospio* sp. n., the bivalve *Limopsis marionensis* exhibited no seasonal variability (Fig. 10). However, isotope values in this species were 2-3‰ enriched in ^{13}C and ^{15}N relative to the other taxa described above, suggesting a more refractory or recycled carbon source. Feeding mode in *L. marionensis* is not definitively known, although many of the suspension-feeding deep-sea bivalves are members of this genus (e.g., Allen, 1979; Oliver, 1979). This species more closely resembles deposit-feeding echiurians in stable isotope values, suggesting a sediment-derived food source such as resuspended sediment particles. Minimal temporal variability in *L. marionensis* may thus reflect the lack of seasonal change in stable isotope values of surface sediments (Fig. 4), consistent with a sediment "food bank."

While some seasonal variations in stable isotope signature were found in the suspension-feeding crinoid *Promachocrinus kerguelensis*, these variations were relatively small, and the crinoids always fell within a range constituting one trophic level above net plankton (Fig. 11). Small differences in $\delta^{13}C$ between spring 1999 and spring 2000 may reflect changes in isotopic values of the algal food source for zooplankton between years (Fig. 2). Variations in crinoid tissues could also reflect seasonal and/or ontogenetic shifts in stable isotopic signatures of krill and other zooplankton (cf., Frazer, 1996; Schmidt *et al.*, 2003).

Implications for benthic-pelagic coupling on the WAP shelf

Values of $\delta^{15}N$ among benthic fauna in our study are depleted compared to deep-sea areas of phytodetritus deposition such as the Porcupine Abyssal Plain (PAP) (Iken *et al.*, 2001). The lack of ^{15}N-enrichment on the WAP shelf and in other high-latitude systems (e.g., Hobson *et al.,* 1995, 2002; Dunton, 2001; Nyssen *et al.*, 2002) strongly suggests that fresh algal material rapidly sinks to the seafloor during summer with minimal degradation in the water column, and enters the benthic food web (see also Smith *et al.*, 2005; Mincks *et al.*, 2005). Further, while $\delta^{13}C$ signatures of plankton samples varied by as much as 14‰ over the course of this study, and sediment trap material by more than 5‰, $\delta^{13}C$ values in surface sediments only varied by about 2‰ (Fig. 3). The close connection between stable isotope values of sediments and those of detritivores, with relatively little temporal variation in stable isotope values of animal tissues, suggests that bloom-derived material is incorporated into the sediment and remains available to consumers throughout much of the year. The stable isotope data, combined with previously reported patterns of labile organic compounds and microbial biomass on the WAP shelf (Mincks *et al.*, 2005), lends additional credence to the hypothesis that a "food bank" of labile material persists in Antarctic shelf sediments across seasons. In addition, our data indicate that WAP shelf sediments and resident detritivores may integrate short-term (seasonal to interannual) variability in flux events, exhibiting substantial "inertia," and responding to ecosystems changes over longer time scales (years to decades) (Smith *et al.*, 2005). The benthic detritivorous community may thus prove useful for monitoring long-term (i.e., low-frequency) changes in WAP shelf ecosystems, such as those resulting from climate change (cf., R. Smith *et al.*, 2003).

Table 1. Mean stable isotope values (‰) and C/N (wt/wt) of particulate organic matter and sediments. Standard errors, where applicable, are indicated in parentheses. Cruise(s) and Station(s) indicate time and place of collection for all samples included in the mean. Cruise I = Nov 99, II = Mar 00, III = Jun 00, IV = Oct 00, V = Mar 01.

Source Material	Cruise	Station	N	$\delta^{13}C$	$\delta^{15}N$	C/N
Ice algae	I	A	1	-19.02	6.02	7.3
	IV	B	1	-19.48	4.51	4.7
Plankton	I	B	1	-27.18	3.67	6.3
		C	2	-33.93 (0.15)	4.32 (1.45)	4.8 (0.15)
	II	A	1	-33.14	5.26	4.1
		B	1	-31.32	5.58	5.5
		C	1	-26.08	4.60	4.4
	III	A	1	-25.70	4.25	4.0
		B	1	-26.88	4.97	5.0
		C	1	-27.30	6.57	4.9
	IV	A	1	-28.85	3.25	4.9
		B	1	-25.83	7.49	4.0
		C	2	-29.56 (3.44)	4.18 (2.37)	4.5 (0.2)
	V	A	1	-14.94	6.80	5.4
		B	1	-18.45	4.20	3.6
		C	1	-29.91	3.21	4.9
Phytodetritus	V	A	2	-22.92 (0.22)	6.23 (0.22)	5.9 (0.6)
		B	2	-25.73 (0.09)	5.66 (0.31)	6.2 (0.03)
		C	1	-25.46	7.92	5.7
Sediment trap	II	B	2	-30.19 (0.17)	1.78 (0.09)	5.8 (0.1)
	III	B	2	-29.58 (0.49)	3.35 (0.24)	6.2 (0.02)
	IV	B	2	-26.80 (0.04)	5.93 (1.09)	5.2 (0.1)
	V	B	2	-27.67 (0.20)	3.06 (0.06)	6.7 (0.1)
Surface sed (0-0.5 cm)	I	A	2	-24.05 (0.03)	4.07 (0.01)	6.8 (0.1)
		B	2	-26.61 (1.63)	4.57 (0.18)	7.4 (0.7)
		C	2	-25.93 (0.57)	4.18 (0.10)	6.8 (0.2)
	II	A	2	-24.38 (0.04)	3.73 (0.24)	6.8 (0.05)
		B	2	-25.03 (0.10)	4.22 (0.20)	6.7 (0.1)
		C	2	-25.29 (0.23)	3.93 (0.46)	6.7 (0.01)
	III	A	2	-24.00 (0.05)	4.25 (0.11)	7.0 (0.05)
		C	2	-25.18 (0.09)	3.61 (0.77)	6.5 (0.06)
	IV	A	2	-24.62 (1.11)	2.77 (0.67)	6.7 (0.2)
		C	2	-25.11 (0.02)	4.34 (0.09)	6.6 (0.06)
	V	A	2	-24.15 (0.22)	6.40 (0.49)	6.3 (0.2)
		B	2	-25.77 (0.42)	4.63 (1.12)	6.1 (0.3)
		C	1	-25.05	5.59	6.0
Subsurface sed. (4-6 cm)	II	A	1	-23.69	4.99	7.2
		B	1	-25.00	6.21	7.0
		C	1	-25.36	8.05	6.4
	V	A	2	-23.40 (0.03)	6.12 (0.41)	6.3 (0.1)
		B	2	-24.88 (0.03)	6.28 (0.55)	6.2 (0.2)
		C	1	-25.08	5.98	6.3

Table 2. Mean stable isotope values (‰) and C/N ratios of benthic invertebrates and fish. Feeding type abbreviations refer to surface deposit feeders (SDF), subsurface deposit feeders (SSDF), suspension feeders (SF), and predators/scavengers (P/S). Numbers in parentheses = ± 1 standard error. N_i = number of individuals.

Species	**Feeding Type**	**N_i**	**$\delta^{13}C$**	**$\delta^{15}N$**	**C/N**
Echinodermata					
Holothuroidea					
Peniagone sp.	SDF	17	-24.45 (0.20)	8.15 (0.19)	3.54 (0.10)
Protelpidia murrayi	SDF	15	-23.54 (0.32)	7.97 (0.22)	3.55 (0.09)
Molpadia musculus	SSDF	5	-18.35 (0.87)	10.16 (0.22)	4.81 (0.17)
Paracucumis antarctica	SSDF	4	-18.88 (0.28)	10.50 (0.54)	4.12 (0.17)
Indet. Synallactid holoth.	SDF	5	-24.22 (0.16)	10.00 (0.25)	3.65 (0.17)
Asteroidea					
Bathybiaster loripes obesus	P/S	5	-22.65 (0.38)	9.17 (0.45)	3.36 (0.12)
Cuenotaster involutus	P/S	5	-22.51 (0.48)	9.86 (0.30)	3.52 (0.04)
Echinoidea					
Amphineustes lorioli	SSDF	5	-25.99 (0.17)	8.60 (0.21)	6.80 (0.59)
Amphineustes rostratus	SSDF	5	-27.16 (0.54)	7.99 (0.27)	7.32 (0.57)
Ctenocidarus perrieri	P/S	5	-21.46 (0.16)	15.58 (0.15)	3.35 (0.61)
Sterechinus antarcticus	P/S	5	-23.60 (0.22)	10.20 (0.32)	2.82 (0.47)
Crinoidea					
Promachocrinus kerguelensis	SF	12	-25.70 (0.26)	8.43 (0.15)	4.22 (0.10)
Mollusca					
Bivalvia					
Limopsis marionensis	SF?	14	-21.87 (0.12)	10.09 (0.09)	3.31 (0.03)
Gastropoda					
Aforia magnifica	P/S	4	-21.28 (0.41)	9.49 (0.43)	3.93 (0.13)
Harpovoluta charcoti	P/S	5	-20.62 (0.65)	10.64 (0.21)	3.70 (0.08)
Cephalopoda					
Pareledone sp.	P/S	7	-24.50 (0.12)	9.12 (0.26)	3.87 (0.64)
Arthropoda					
Pycnogonida					
Colossendeis sp.	P/S	5	-25.98 (0.18)	7.27 (0.36)	3.97 (0.08)
Amphipoda					
Natatolana meridionalis	P/S	4	-23.91 (0.99)	7.95 (0.66)	4.69 (0.15)
Cnidaria					
Anthozoa					
Hormathia lacunifera	P/S	4	-22.16 (0.22)	8.87 (0.18)	3.09 (0.28)
Isosycionis alba	P/S	5	-26.52 (0.51)	8.32 (0.35)	4.48 (0.15)

Table 2 (cont.).

Species	Feeding Type	N_i	$\delta^{13}C$	$\delta^{15}N$	C/N
Annelida					
Polychaeta					
Laetmonice producta	P/S	4	-23.60 (0.78)	11.40 (0.66)	3.63 (0.15)
Aurospio sp. n.	SDF	12	-24.98 (0.04)	7.85 (0.06)	3.55 (0.13)
Echiuria					
Echiurian indet.	SDF	4	-21.27 (1.10)	10.15 (0.63)	3.34 (0.12)
Porifera					
Cinachyra antarctica	SF	4	-21.63 (0.53)	16.47 (0.18)	3.94 (0.14)
Vertebrata					
Osteichthyes					
Licodichthys sp. (eelpouts)	P/S	5	-24.23 (0.53)	10.62 (0.73)	3.46 (0.10)
Nototheniid sp.	P/S	5	-24.86 (0.30)	10.65 (0.30)	3.45 (0.09)
Chiondraco rastrospinosus (ice fish)	P/S	5	-25.88 (0.12)	7.64 (0.19)	3.38 (0.05)

Table 3. Statistically significant seasonal differences in $\delta^{13}C$ and $\delta^{15}N$ for *Peniagone* sp. (SDF), *Protelpidia murrayi* (SDF), and *Promachocrinus kerguelensis* (SF), based on Multivariate ANOVA LSD *post-hoc* comparisons. Significant differences for each isotope are marked with C or N, as well as asterisks representing the significance level (e.g., $p = 0.05$ (C*), 0.01 (C**) and <0.001 (C***)). $\delta^{13}C$ comparisons are recorded left-to-right, and $\delta^{15}N$ comparisons are recorded top-to-bottom. x = not significant; nd = no data.

		Nov-99	Mar-00	Jun-00	Oct-00	Mar-01
Peniagone sp.	Nov-99	x				
	Mar-00	x	x			
	Jun-00	x	x	x		
	Oct-00	nd	nd	nd	nd	
	Mar-01	N**	N*	N**	nd	x
Protelpidia murrayi	Nov-99	x	C**	C*	nd	x
	Mar-00	N*	x	x	nd	C**
	Jun-00	x	x	x	nd	x
	Oct-00	nd	nd	nd	nd	nd
	Mar-01	N***	N**	N**	nd	x
P. kerguelensis	Nov-99	x				
	Mar-00	nd	nd			
	Jun-00	x	nd	x		
	Oct-00	x	nd	N*	x	
	Mar-01	N**	nd	N**	x	x

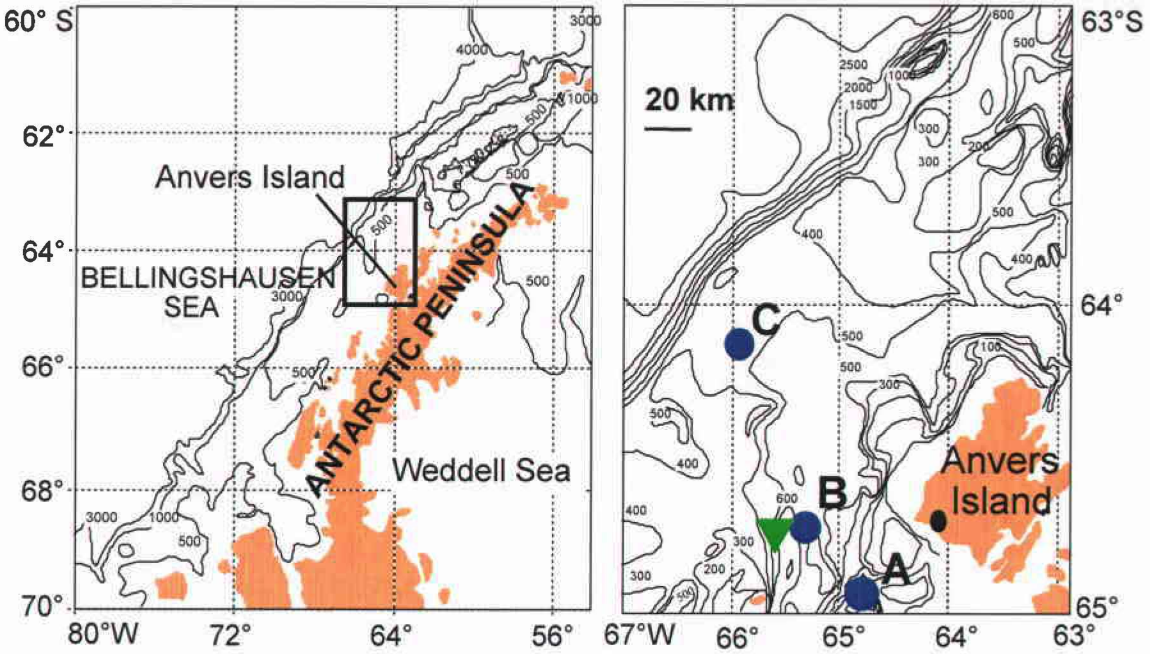

Fig. 1. Map of the study area. (●) Locations of Stations A, B, and C; (▼ST) Location of sediment trap mooring. Depth contours are in meters.

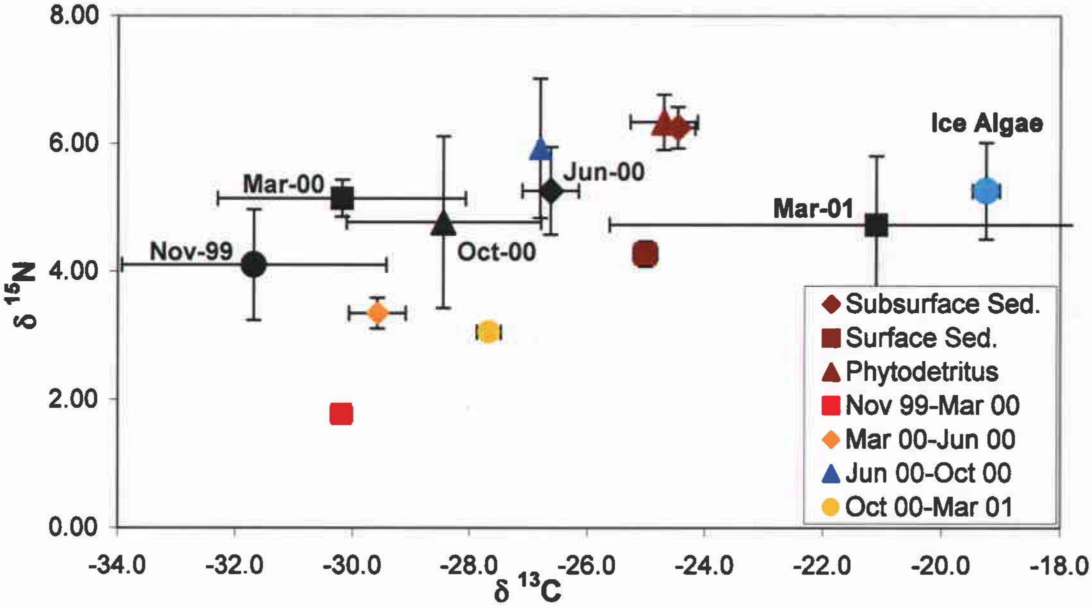

Fig. 2. Mean stable isotope values ($\delta^{15}N : \delta^{13}C$) for net-collected plankton (means of all three stations; **black** symbols) and ice algae (Nov 99 and Oct 00) (●), sediment trap samples (■, ◆, ▲, ●; mean of top and bottom trap), and sediments and phytodetritus (**brown** symbols; means of all stations and time points). Error bars indicate ± 1 standard error.

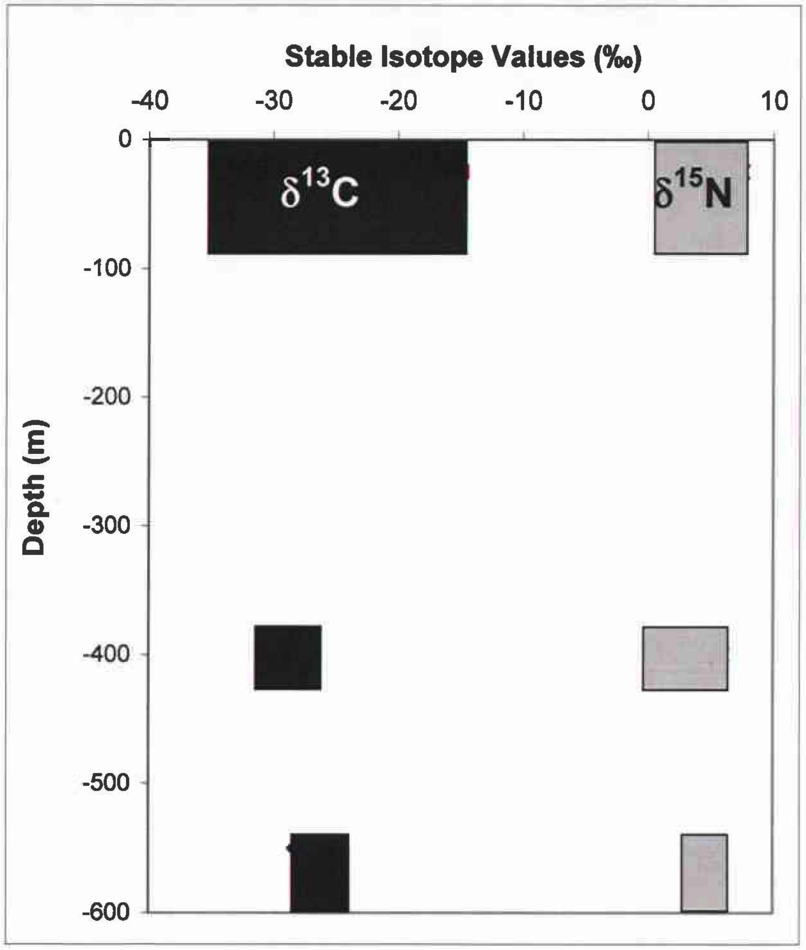

Fig. 3. Range of stable isotope values measured at all time points for carbon (black bars) and nitrogen (gray bars) at various sampling depths, including net collected plankton (~10-100 m), sediment traps (mean of traps at 150 and 170 m above seafloor), and Station B surface sediments (~550 m; area beneath sediment traps).

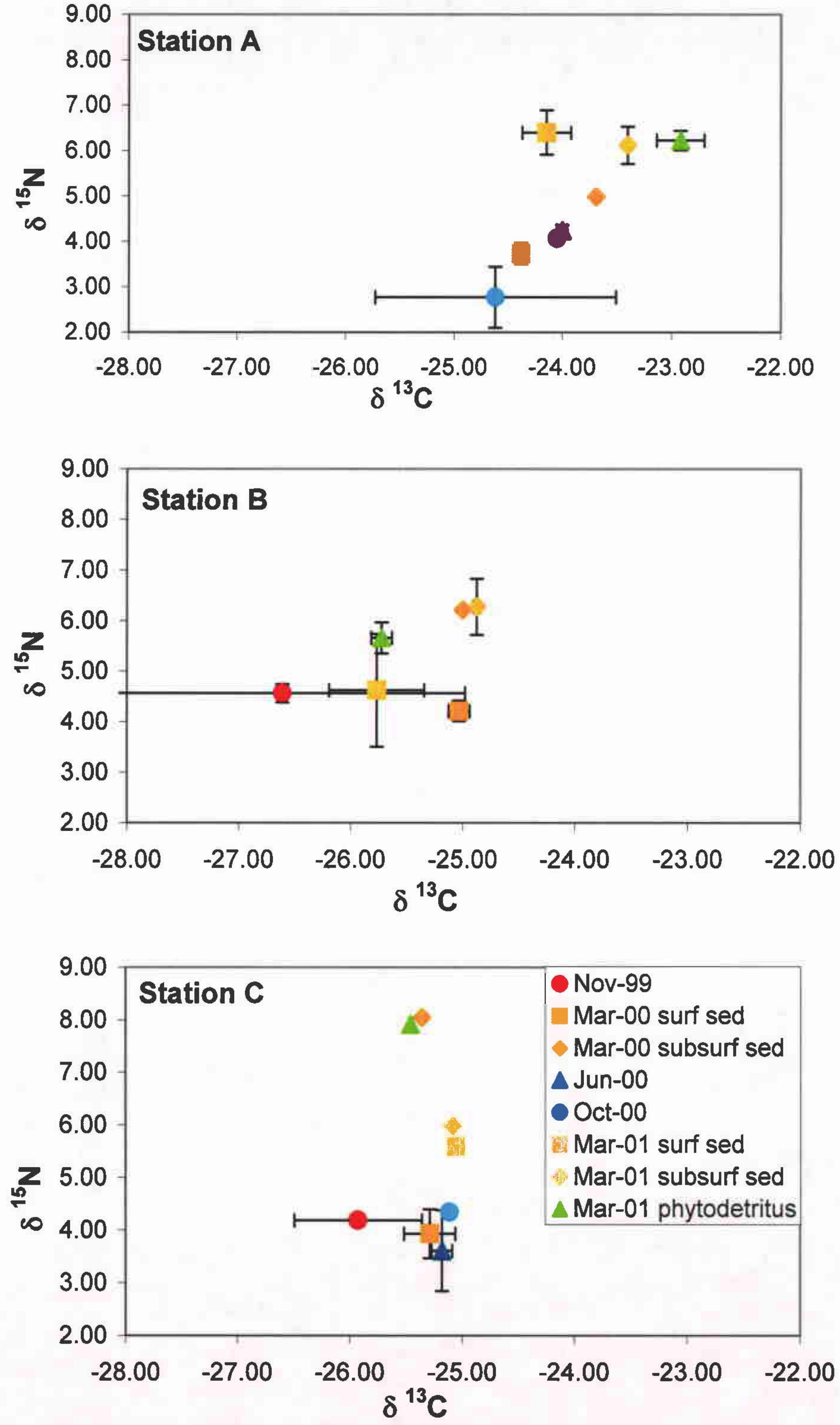

Fig. 4. Mean stable isotope value ($\delta^{15}N : \delta^{13}C$) of surface sediments (0-0.5 cm) and subsurface sediments (4-6 cm; Mar 00 and Mar 01 only) at (a) Station A, (b) Station B, and (c) Station C in all seasons. Error bars indicate ± 1 standard error. n = 2 (except Stn. C, Mar 01 where n = 1).

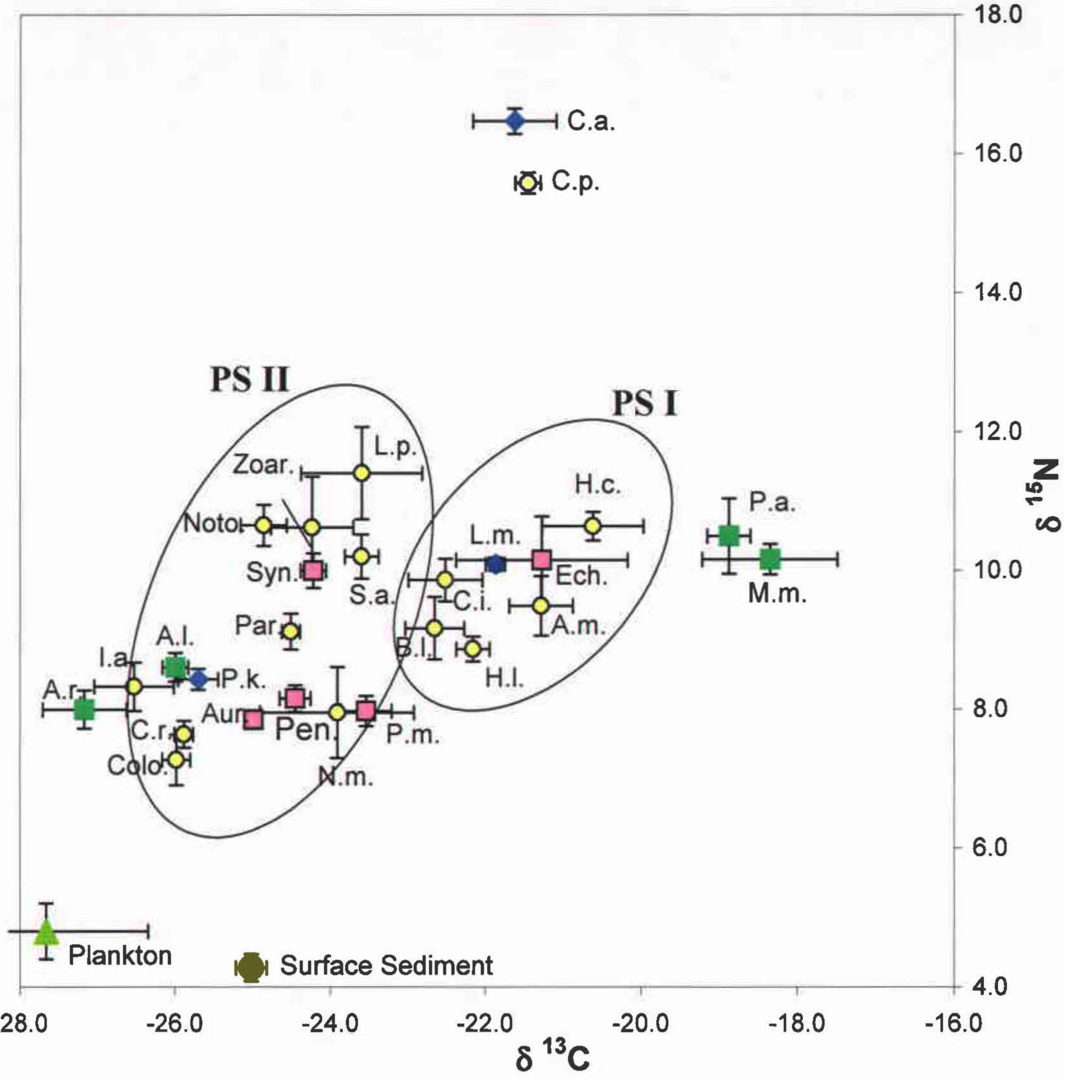

Fig. 5. Mean stable isotope values ($\delta^{15}N$: $\delta^{13}C$) for benthic fauna, with average surface sediment and net plankton values. Points represent overall means, including all stations and cruises. Symbols refer to feeding type (● = Predators/Scavengers; ■ = Subsurface Deposit Feeders; ■ = Surface Deposit Feeders; ♦ = Suspension Feeders). Ovals labeled P/S I & II indicate members of predator/scavenger groups I & II (see text). Error bars indicate ± 1 standard error, n=4 to 13. Abbreviations are as follows: A.l.= *Amphineustes lorioli*; A.m.= *Aforia magnifica*; Aur.= *Aurospio* sp. n.; A.r.= *Amphineustes rostratus*; B.l.= *Bathybiaster loripes*; C.a.= *Cinachyra antarctica*; C.i.= *Cuenotaster involutus*; Colo.= *Colossendeis* sp.; C.p.= *Ctenocidaris perrieri*; C.r.= *Chiondraco rastrospinosus*; Ech.= Indet. green echiurian; H.c.= *Harpovoluta charcoti*; H.l.= *Hormathia lacunifera*; I.a.= *Isosycionis alba*; L.m.= *Limopsis marionensis*; L.p.= *Laetmonice producta*; M.m.= *Molpadia musculus*; N.m.= *Natatolana meridionalis*; Noto.= Nototheniid sp.; P.a.= *Paracucumis antarctica*; Par.= *Pareledone* sp.; Pen.= *Peniagone* sp.; P.k.= *Promachocrinus kerguelensis*; P.m.= *Protelpidia murrayi*; S.a.= *Sterechinus antarticus*; Syn.= Synallactid holothurian; Zoar.= Zoarcids (eelpouts; *Licodichthys* sp.)

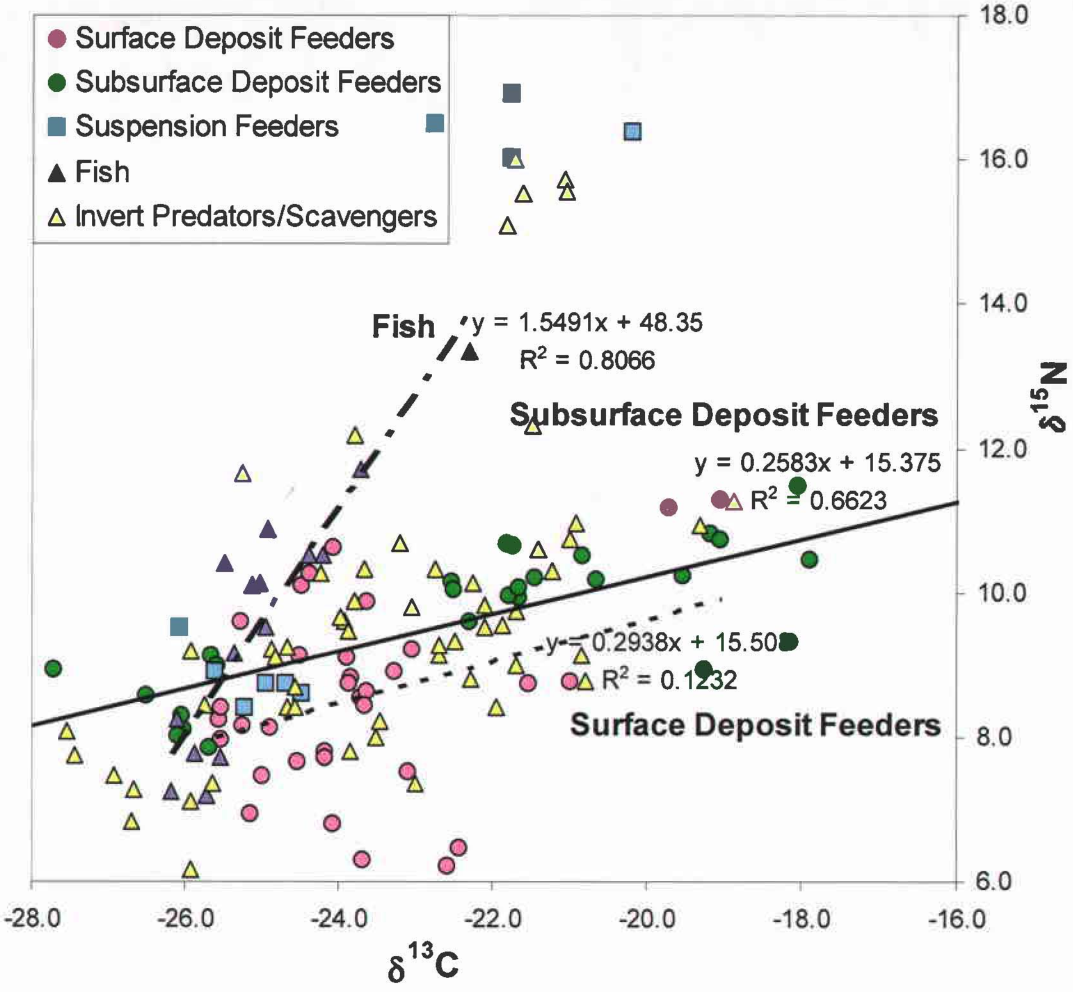

Fig. 6. Stable isotope ratios ($\delta^{15}N$:$\delta^{13}C$) of each individual organism, with trend lines associated with major trophic groups.

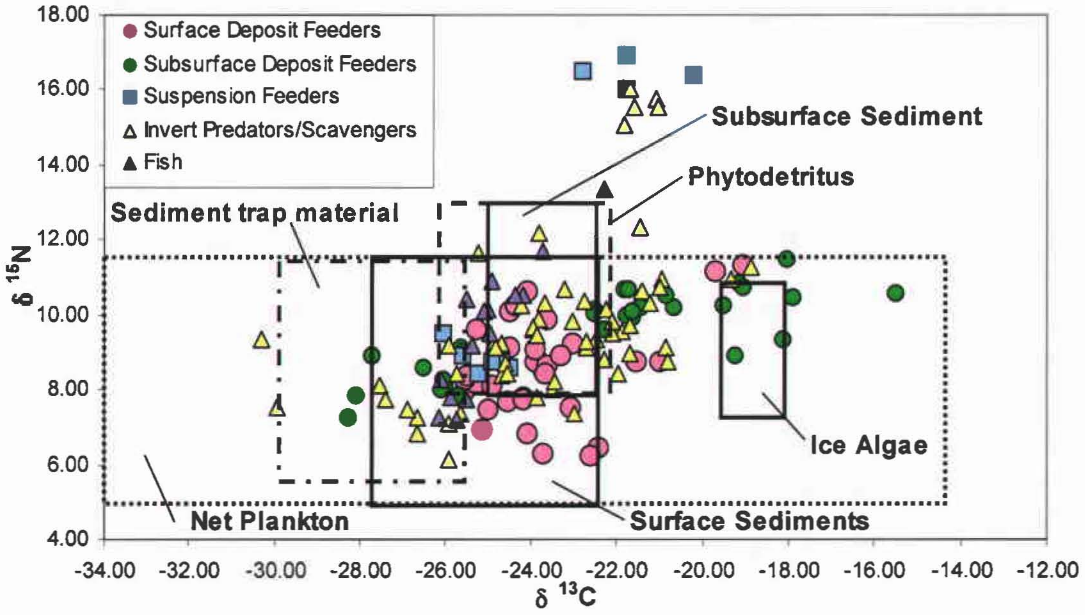

Fig. 7. Stable isotope ratios ($\delta^{15}N:\delta^{13}C$) of each individual organism analyzed, with "trophic shift" boxes (3-5‰ for $\delta^{15}N$ and 0-1‰ for $\delta^{13}C$) indicating expected range of values for organisms feeding exclusively on particular sources of organic material .

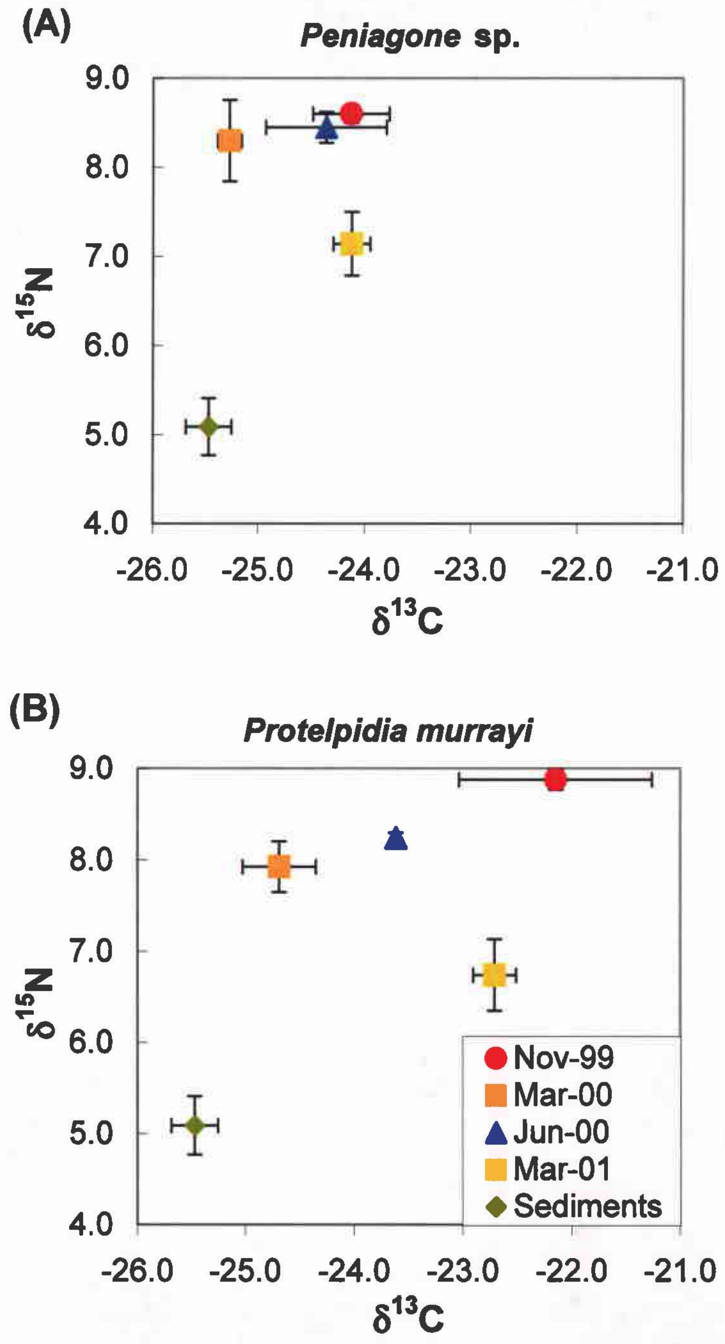

Fig. 8. Stable isotope ratios ($\delta^{15}N:\delta^{13}C$) of two deposit-feeding holothurians and surface sediments (0-0.5 cm). A) *Peniagone* sp.; B) *Protelpidia murrayi*. Error bars indicate ± 1 standard error.

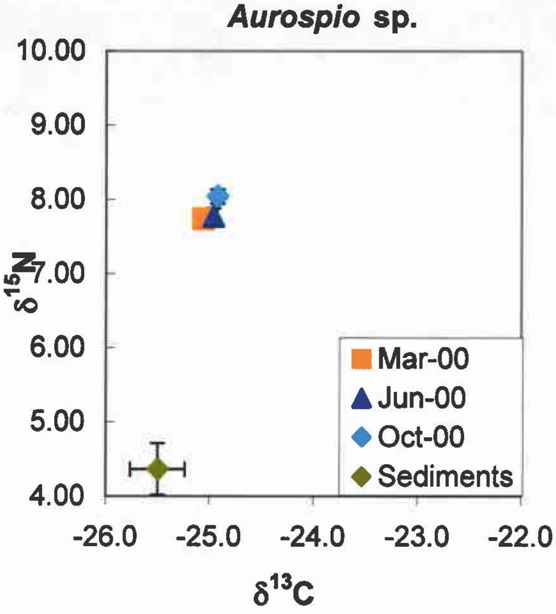

Fig. 9. Stable isotope ratio ($\delta^{15}N:\delta^{13}C$) of deposit-feeding spionid polychaetes, relative to surface sediments (0-0.5 cm). Error bars indicate ± 1 standard error.

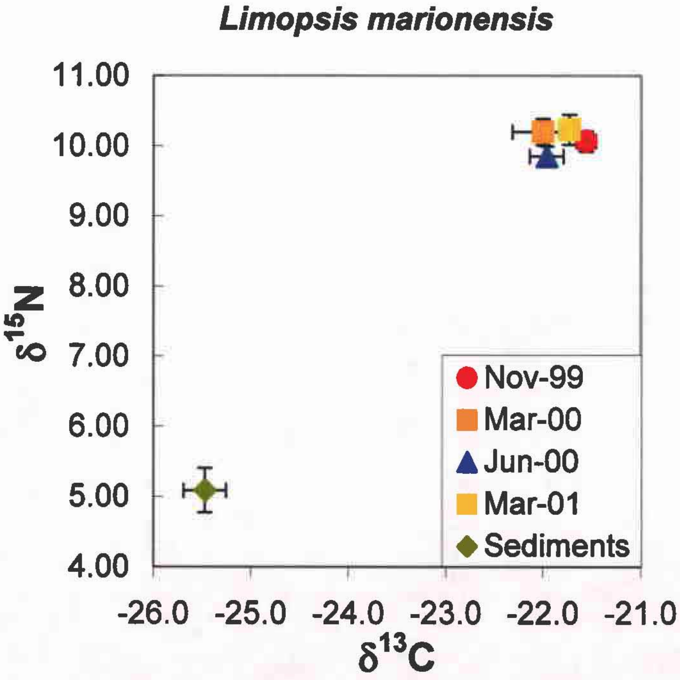

Fig. 10. Stable isotope ratio ($\delta^{15}N:\delta^{13}C$) of the bivalve, *Limopsis marionensis*, relative to surface sediments (0-0.5 cm). Error bars indicate ± 1 standard error.

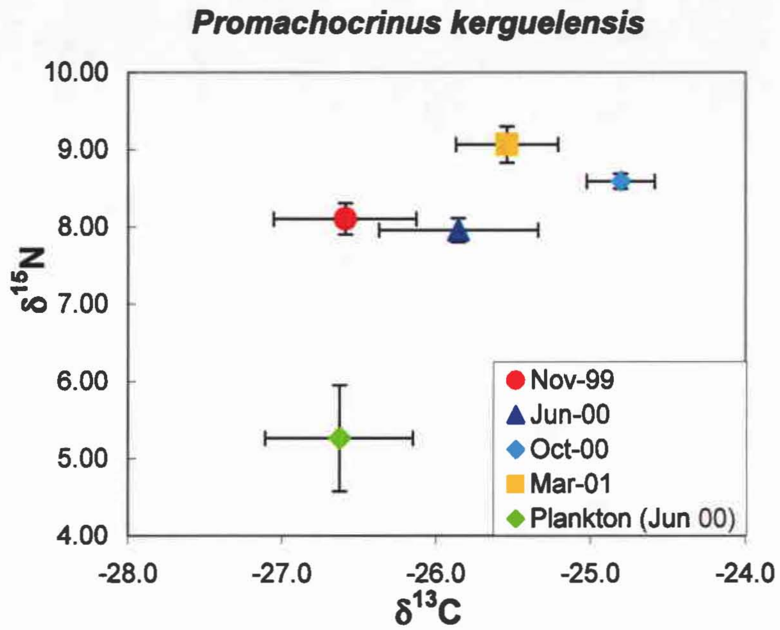

Fig. 11. Stable isotope ratio ($\delta^{15}N:\delta^{13}C$) of the suspension-feeding crinoid, *Promachocrinus kerguelensis*, relative to Jun 00 plankton (primarily zooplankton). Error bars indicate ± 1 standard error.

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CHAPTER 4. RECRUITMENT PATTERNS IN ANTARCTIC SHELF SEDIMENTS: LINKS BETWEEN PHYTODETRITUS DEPOSITION AND REPRODUCTIVE STRATEGIES

ABSTRACT

Summer phytoplankton blooms on the West Antarctic Peninsula (WAP) shelf result in episodic deposition of labile food material for benthic detritivores. The presence of a highly seasonal food source has been hypothesized to affect reproductive behavior and timing of recruitment events for WAP benthos. In particular, the presence of particulate food in the water column (i.e., blooming phytoplankton) may influence the success of planktotrophic larval stages, or bloom-derived phytodetritus at the seafloor may support recruitment of benthic juveniles. Juvenile macro- and megafauna (>100 μm) were collected from megacores in a seasonal time-series sampling program at three stations on the WAP continental shelf. Juvenile macrofauna consisted largely of Annelida (polychaetes and oligochaetes), and abundant megafaunal juveniles included Bivalvia, Nemertea, Sipuncula, Holothuroidea, and Anthozoa. A total of 4098 juvenile macro- and megafauna were collected (average densities of 2000 to 7000 m^{-2}), with overall composition dominated by polychaetes (2581 individuals). Seasonal patterns of abundance were observed in 11 of 14 families of macrofaunal polychaetes, although these patterns were largely confined to particular stations. The majority of polychaete taxa showed recruitment peaks in Oct 2000, prior to the onset of the summer phytoplankton bloom, while some taxa exhibited peak juvenile abundance in summer months (Mar 2000 and 2001). Based on observed abundance patterns, polychaetes are classified into “seasonal”, “marginally seasonal”, and “non-seasonal” reproductive types. Three megafaunal taxa also showed statistically significant peaks in juvenile abundance at particular locations, largely in summer months. However, observed seasonal reproductive patterns in megafauna appear likely to be linked to seasonal detritus deposition in terms of gametogenesis, rather than recruitment of juveniles. A variety of factors, in addition to seasonal food availability, may influence recruitment dynamics on the WAP shelf, including food-related recruitment bottlenecks, post-settlement predation, and advective influx or efflux of larvae from other shelf or deep-sea locations.

INTRODUCTION

Antarctic continental-shelf sediments receive intense seasonal pulses of particulate organic flux derived from summer phytoplankton blooms in December-March, following the retreat of winter sea-ice (e.g., Smith *et al.*, 1996), with sinking particle fluxes orders of magnitude larger than during ice-covered winter months (Wefer *et al.*, 1988; Dunbar *et al.*, 1989; Honjo, 1990). These dramatic productivity pulses result in deposition of labile food material for benthic detritivores (Chapter 2; Smith *et al.*, 2005; Smith and DeMaster, in review). Further, polar habitats such as the Antarctic shelf are characterized by consistently low bottom water temperatures, and are generally considered oligotrophic for most of the year. Polar shelf habitats have thus been likened to deep-sea regions, which are now known to experience episodic deposition of organic material in many areas (e.g., Tyler, 1988; Smith, 1994; Beaulieu, 2002).

The presence of a highly seasonal food source has the potential to influence benthic ecological processes such as gametogenesis, spawning, and recruitment (Tyler *et al.*, 1982; Tyler, 1988; Clarke, 1992), but evidence of a direct correlation between reproductive cycles and organic nutrient flux in polar habitats is somewhat equivocal (Pearse *et al.*, 1991; Clarke, 1992; Tyler *et al.*, 1994; Ambrose and Renaud, 1997). Seasonal bloom dynamics might be expected to influence the timing of recruitment to the benthos if the presence of particulate food in the water column (i.e., blooming phytoplankton) influences the success of planktotrophic larval stages, or if bloom-derived phytodetritus at the seafloor supports recruitment of benthic juveniles during nutritional bottlenecks in their life history (e.g., Hentschel, 1998a; 1998b). Alternatively, phytodetritus pulses could act on adults, either releasing vitellogenic (i.e., egg production) processes from food limitation, or merely serving as a cue to synchronize gamete production and/or spawning among individuals of a population (e.g., Tyler, 1988; Gooday and Turley, 1990; Eckelbarger and Watling, 1995).

Direct impact of food availability for *adult* benthic detritivores as a selective force in determining reproductive or developmental strategies has received relatively little attention. Nonetheless, parameters such as egg size, which appears be directly related to larval developmental mode (i.e., feeding vs. non-feeding) (e.g., Emlet *et al.*, 1987; Sinervo and McEdward, 1988), must be influenced by parental nutrition on some level. Indeed, recent work with echinoderms has shown that parental nutrition can impact egg size and biochemical content, as well as larval growth rate and time to settlement (George *et al.*, 1990, 1991; George, 1990, 1996; Bertram and Strathmann, 1998; Emlet and Hoegh-Guldberg, 1997).

The relative importance of larval and adult nutrition in determining life history strategies may be influenced by the spatial and temporal separation of food sources for different life history stages. In an environment with a relatively rich and predictable sediment "food bank" for benthic detritivores, such as that on the WAP shelf (Chapter 2), a less predictable larval food supply could select for a greater level of initial parental investment, and result in a higher incidence of brooding and/or lecithotrophic forms. Alternatively, rapidly reproducing species such as macrofaunal polychaetes may exploit seasonal food pulses, producing smaller eggs (i.e., with less parental investment) that give rise to planktotrophic larvae.

The fact that some Antarctic benthos appear to release planktotrophic larvae in winter when planktonic food is scarce (Clarke, 1992; Stanwell-Smith and Peck, 1998) seems to support the contention that summer blooms are *not* the controlling mechanism for seasonal larval production in all species. Recent work on the WAP shelf suggests extended vitellogenic cycles in some echinoderms that appear to be linked to the seasonal bloom cycle (Galley, 2003; Johnson *et al.*, 2005). Further, low temperatures allow for low metabolic rates in polar larvae, which may increase their potential to survive for extended periods (months to years) without necessarily relying on particulate food resources (e.g., Shilling and Manahan, 1994). For example, the Antarctic sea urchin *Sterechinus neumayeri* does not necessarily require particulate food for completion of early developmental stages, because low metabolic rates allow larvae to utilize endogenous resources to reach a late planktotrophic (i.e., feeding) larval stage (Marsh and Manahan, 1997; Marsh *et al.*, 1999).

Recruitment to benthic habitats has been little studied in Antarctic waters, and the minimal data available refer to shallow, hard-substrate environments. These studies suggest only weak coupling between recruitment events and summer phytoplankton blooms. Stanwell-Smith and Barnes (1997) conducted shallow-water (5-25 m) settling-plate studies for 21 months at Signy Island, concluding that the dominant settling taxa (bryozoans and spirorbid polychaetes) essentially recruited at low rates throughout the year. McClintock *et al.* (1988) also concluded that the common Antarctic asteroid *Odontaster validus* recruits at low levels year-round in McMurdo Sound. Most recently, Bowden (2005) conducted the first detailed study of recruitment of benthos within the Antarctic Circle (67.5^{o}S near Adelaide Island), where bryozoans and spirorbid polychaetes dominated the 39 taxa recovered from settling plates. Most species settled throughout the year, but there was a clear seasonal pattern with a peak number of taxa recruiting in late winter.

I present data from a seasonal time-series study at three stations on the deep (~600 m) Antarctic continental shelf. To my knowledge, this is the first recruitment study conducted in a deep, soft-sediment region of the Antarctic shelf. My objectives were to (1) examine temporal patterns of recruitment in benthic macro- and megafauna, (2) explore relationships between seasonal recruitment events and life-history strategies, and (3) establish linkages between summer phytodetritus deposition and benthic recruitment patterns. The presence of a persistent sediment "food bank" has recently been established at these locations (Chapter 2; Mincks *et al.*, 2005a). Thus, I predicted a tendency toward higher levels of parental investment, with limited correlation between seasonal phytodetritus deposition and benthic recruitment for most detritivorous taxa.

MATERIALS AND METHODS

Study site

Samples were collected as part of the FOODBANCS program (Smith and DeMaster, in review), on a series of five cruises to the West Antarctic Peninsula (WAP) shelf, as described in detail in Chapter 2. Seasonal time-series sampling encompassed two summer bloom periods, occurring in (I) Nov/Dec 1999 (summer pre-bloom season), (II) Mar 2000 (end of the summer bloom), (III) Jun 2000 (winter oligotrophic period), (IV) Oct 2000 (end of winter, during winter sea-ice retreat) and (V) Feb/Mar 2001 (during summer bloom) (Fig. 2.2). Three stations (A, B, and C) were sampled on a northwest to southeast transect across the continental shelf from Anvers Island (Fig. 3.1; Table 2.1).

Seasonal bloom dynamics and the timing of phytodetritus deposition at FOODBANCS study sites are described in detail in Chapter 2 and elsewhere (Mincks *et al.*, 2005a; Smith *et al.*, 2005; Smith and DeMaster, in review). Briefly, seasonal dynamics in the flux and fate of organic material in sediments was determined by comparing Chl-*a* flux to sediment traps with temporal patterns in inventories of Chl-*a* and enzymatically hydrolysable amino acids (EHAA) (Mayer *et al.*, 1995) in sediments. While particulate flux increased in summer months (Dec to Mar), a much larger flux event occurred in the second summer season sampled (2000/2001) (Fig. 2.3). This event also resulted in large interannual variability in phytodetrital accumulation between summer 2000 and 2001 (Smith and DeMaster, in review). While, at most, minimal phytodetritus appeared on the sediment surface during the summer 1999/2000, in the following year, a thick phytodetrital carpet (~1-5 cm) was visible in bottom photographs and megacore samples. FOODBANCS results thus indicated significant seasonal variability in vertical flux of Chl-*a* to the WAP shelf, although interannual differences in flux were far greater than seasonal differences during the study period (Fig. 2.5). Despite the large temporal variability in flux, seafloor concentrations and inventories of labile compounds such as Chl-*a* (Fig. 2.4 and 2.5) and EHAA (Fig. 2.6 and 2.7) varied modestly, particularly below the top few centimeters of sediment. This dampened seasonal and interannual variability in sedimentary organic pools is thought to constitute a sediment "food bank" available to benthic detritivores throughout low-flux months (or years) (Chapter 2; Mincks *et al.*, 2005a).

Field and laboratory methods

On each cruise, sediment tube cores (10-cm diameter) were collected with a Bowers & Connelly Megacorer from each of at least five randomly located deployments at each station. Overlying water was siphoned off the top of each core and filtered with a 63-μm sieve. Cores were sliced into two discrete horizontal layers, from 0-1 and 1-5 cm depth. After slicing, each sediment layer was transferred whole into a separate jar, and preserved in 10% formalin solution.

Upon return to the laboratory, samples were sieved on both a 300- and 100-μm sieve, transferred to 80% ethanol, and stained with Rose Bengal prior to sorting under a dissecting microscope. Organisms in the 100 to 300-μm size fraction were assumed to be juvenile macro- and megafauna (adults of which are operationally defined as 300 μm to 3 cm, and >3 cm, respectively). Juvenile macrofauna consisted largely of Annelida (polychaetes and oligochaetes), for which juvenile stages are typically delineated based on the numbers of setigers. The operational definition of juveniles used here is likely biased toward low abundances, since the vast majority of individuals analyzed were at stages with <10 setigers, i.e., much smaller than many "juvenile" polychaetes described in the literature (e.g., Blake, 1996b; 1999).

Additional juvenile megafauna were also collected in the larger size fraction (>300 μm), including Holothuroidea, Bivalvia, Sipuncula, and Nemertea. While Glover *et al.* (2005) published overall macrofaunal (>300 μm) community dynamics elsewhere, these select megafaunal taxa are included in the recruitment analysis under the assumption that their small size indicates recent colonization. Thus, temporal patterns in recruitment of major megafaunal taxa were determined by comparing abundance of all juveniles >100 μm across seasons. Meiofaunal taxa (63-300 μm, e.g., foraminifera, copepods, nematodes) were not considered here (but see Suhr *et al.*, 2003).

Length-frequency measurements were performed for bivalves, as well as the holothurian *Protelpidia murrayi*, in order to determine if seasonal abundance increases were related to settling of distinct cohorts. Bivalves were measured only at Station A, where they were most abundant (n = 302), and where statistically significant temporal variability was detected. Due to low abundances (n = 63), all individuals of *P. murrayi* were measured. Despite these low abundances, *P. murrayi* was selected due to the reasonable level of certainty in identification at the species level, as well as the abundant ancillary data available to facilitate interpretation of observed patterns (e.g., Galley, 2003; Sumida *et al.*, 2005).

One-way ANOVAs were performed for each taxon at each station to test for temporal differences in abundance of juveniles (Sokal and Rohlf, 1995). Significance was determined using α-levels of 0.10. However, the large number of tests performed (n = 75) indicates a high probability of committing Type I errors. Methods for avoiding multiple-testing effects are controversial (e.g., Harris, 1975) and were not strictly applied here. However, it should be noted that applying a Bonferroni correction for multiple testing effects calls for lowering of the α-level to 0.001 (Harris, 1975; Sokal and Rohlf, 1995).

RESULTS

A total of 2868 individual "juveniles" (100-300 μm) were collected from 74 megacore samples, yielding average juvenile densities ranging from about 2000 to 7000 m^{-2}. These individuals included taxa from at least seven phyla, with overall composition overwhelmingly dominated by polychaetes (2581 individuals). At Station A, 98% of these juveniles were polychaetes, with 81% polychaetes at Station B, and 92% at Station C. At least 21 polychaete families are represented in this collection (Fig. 1). Abundant non-polychaete groups in this size fraction included Anthozoa, Tanaidacea, Bivalvia, Holothuroidea, and Oligochaeta (Fig. 2). In addition, 1230 juvenile megafauna were removed from the >300 μm megacore samples, including Anthozoa, Bivalvia, Nemertea, Sipuncula, and Holothuroidea.

While composition of the Polychaeta was roughly similar at Stations B and C, these stations differed somewhat from Station A (Fig. 1). Paraonidae were the most common polychaete family in the 100-300 μm fraction at all three stations (~30%). At Station A, Syllidae were also dominant (~29%), followed by Opheliidae and Cirratulidae

(~10% each). Syllidae were also abundant at Stations B and C (~15%), but other families, including Acrocirridae, Ampharetidae, Sabellidae, and Chrysopetalidae, showed greater dominance.

Seasonal abundance patterns of juvenile macrofauna

Overall abundance of juvenile polychaetes (100-300 μm) in the top 5 cm of sediment varied significantly with season only at Stations A and C (One-way ANOVA; Table 1), with peak abundances detected in Oct 00 (late winter) (Fig. 3). In addition, seasonality was detected in several individual polychaete families, most of which followed this same abundance trend with seasonality limited to Stations A and C, and peaks most often occurring in Oct 00. Oligochaetes, in contrast, showed a moderately strong trend when data from all stations were combined (One-way ANOVA, $p = 0.093$), but no significant temporal variation when stations were examined individually (Table 1). The overall trend in oligochaetes was probably driven by relatively high abundances at Stations B and C in spring and summer (Oct-Mar) 2000/2001 (Fig. 4).

As suggested by temporal patterns in total juvenile polychaete abundance, most of the variability detected in abundances of individual polychaetes taxa occurred at Stations A and C, with one species (Acrocirrid sp. A) showing seasonality only at Station B (Table 1; Fig. 5). Only one taxon (Paraonid sp. B) showed statistically significant temporal variability at all three Stations (Table 1; Fig. 6). Five taxa showed seasonal recruitment patterns only at Station C (nearest the shelf-break), including Ampharetid sp. B, Chrysopetalids, Cirratulids, Dorvilleids, and Syllids. All these taxa peaked in abundance during Oct 00, with some also showing secondary peaks in Mar 00 or Mar 01

(Table 1; Figs. 7-10). However, if a Bonferroni correction is applied (e.g., Harris, 1975; Sokal and Rohlf, 1995), significant results where $0.10 > p > 0.001$ (e.g., Acrocirrid spp., Table 1) should be considered with caution. Lumbrineridae, Sabellidae, and Spionidae were the only three families not showing any significant temporal variability at any location (Table 1; Fig. 11). Interestingly, this group includes two of the three suspected brooders (Spionidae and Sabellidae) included in this study (Rouse and Fitzhugh, 1994; Gambi *et al.*, 2000; A. Glover, unpublished observations).

Two distinct morphological types (potentially species and thus called Species A and B) of Ampharetidae, Acrocirridae, and Paraonidae were distinguishable among the 100-300 μm juvenile polychaetes, with each type exhibiting seasonality at different locations (Table 1). Acrocirrid sp. A recruited at Station B in Mar 01 (heavy phytodetritus cover), whereas sp. B recruited at Stations A and C in Oct 00 (late winter) (Fig. 5). Ampharetid sp. A recruited at Station A in Oct 00, whereas sp. B recruited at Station C in Oct 00 (Fig. 7). Paraonid sp. B showed seasonality at all three stations, with a distinct peak in abundance in Mar 00 at Station A, and a continuous increase in abundance through the sampling period into Mar 01 at the other two stations (Fig. 6).

Two distinct morphological types of Opheliidae also occurred in these samples, with overwhelming dominance by Type A (cf., Vanreusel *et al.*, 2001). Opheliid Type B closely resembled opheliids found in the "adult" (>300 μm) size fraction, whereas Type A did not resemble any of the adult taxa. The small number of Type B specimens (n = 18) was insufficient for statistical analysis of temporal patterns. However, Opheliid Type A showed a sharp peak in abundance in Jun 00 (mid-winter) at Station A, but occurred at consistently low levels year-round at the other stations (Table 1; Fig. 12).

Seasonal abundance patterns in juvenile megafauna

Among the megafauna, only Bivalvia, Nemertea and Anthozoa showed statistically significant seasonal changes in abundance at some stations (Table 2; Fig. 13). Mirroring trends in the Annelida, seasonal variability occurred at Stations A and C, with no taxa showing statistically significant patterns at Station B.

Bivalve juveniles varied significantly in abundance only at Station A, where peak abundance occurred in summer (Mar) 2000 (Fig. 13). Anthozoa showed similar seasonal peaks in abundance in summer (Mar 00 and 01), with *post hoc* tests (Least Significant Difference, LSD) indicating statistically significant differences between Mar 01 and all other seasons (Fig. 13). Nemerteans showed significant seasonal variability at Stations A and C, with peak abundances in spring (Nov) 1999, followed by steady decline through the remainder of the sampling period (Fig. 13).

Two distinct holothurian taxa were distinguishable in megacore samples. These taxa are believed to be juveniles of the two abundant trawl-collected holothurians, *Protelpidia murrayi* and *Peniagone* sp. Statistical tests did not show significant variability in overall abundance of holothurians over time (Table 2). However, juvenile *Protelpidia murrayi* (a seasonal spawner; Galley *et al.*, 2005) appeared to increase in abundance in winter (Jun-Oct) 2000, particularly at Station B, whereas *Peniagone* sp. did not show any seasonal trends (Fig. 14). Low numbers of individuals and large variance likely confounded tests of statistical significance in these patterns.

Length-frequency analyses in the megafauna

Length-frequency plots for *P. murrayi* juveniles indicate smallest individuals in Mar 00, with peak abundance in the 1000-1500 μm size range at this time (Fig. 15). The number of individuals in size classes up to about 3000 μm increased through Jun and Oct 00. Very small individuals (500-1500 μm) peak in abundance again in Mar 01. While trends are extremely speculative due to low abundances, data suggest recruitment prior to Mar of juveniles with minimum length <1000 μm.

The population of juvenile bivalves at Station A (Fig. 16) appears to consist of multiple cohorts. Recruitment most likely occurs in the 500-1000 μm size range, with maximum abundances in this size class occurring in summer months. Abundances in this size range are high year-round, with peaks in Mar 00, Oct 00, and Mar 01. Thus, while temporal variability was observed, patterns were not necessarily seasonal, and recruitment appears to have occurred throughout the year.

DISCUSSION

A number of juvenile macro- and megafaunal taxa exhibited temporal variability in abundance in West Antarctic Peninsula (WAP) shelf sediments, including bivalves, anthozoans, nemerteans, and several polychaete families (Tables 1 and 2). This variability constitutes evidence of seasonal recruitment pulses in select taxa, and at select locations. All three megafaunal taxa with seasonal abundance trends appeared to recruit most heavily during the summer phytoplankton bloom pulse, although juveniles were present, and thus recruitment occurred, throughout the year. Eight of the nine families of macrofaunal polychaetes showing evidence of seasonal recruitment peaked in abundance in Oct 00, with much of this seasonality occurring near the shelf-break at Station C. However, even for those species showing the most temporal variability, juveniles were present throughout the year. Further, when juvenile abundances at "off-peak" recruitment times are summed, they exceed abundance during recruitment peaks, suggesting continuous recruitment with localized enhancement during particular seasons. Eight of the nine families exhibiting seasonal patterns in abundance of juveniles are thought to produce larvae with at least a short planktonic (either feeding or non-feeding) larval stage, whereas two of the three taxa lacking seasonal patterns are suspected brooders.

Reproductive periodicity in Antarctic marine invertebrates has been the subject of much discussion in recent years (e.g., Clarke, 1988; Pearse *et al.*, 1991; Clarke, 1992). However, temporal patterns of recruitment have been little studied in high-latitude waters. Ambrose and Renaud (1997) looked for seasonal recruitment patterns of polychaetes in an Arctic polynya, reporting multiple "seasonal" recruitment peaks in the relatively short sampling period from May to August. In Antarctic waters, studies have been limited to a few shallow-water settling plate studies (Dayton, 1989; Stanwell-Smith and Barnes, 1997; Bowden, 2005), leaving recruitment to the extensive soft-sediment shelf habitats largely unexplored.

Reproductive responses to phytodetritus deposition

If detritivore food resources are limited in Antarctic sediments, the summer phytodetritus pulse to the Antarctic continental shelf may constitute a major source of nutrition for the initiation of gametogenesis. In this case, seasonal patterns in spawning might be expected, whereby the phytodetritus pulse provides the necessary nutrient reserves to initiate gametogenesis, and spawning occurs synchronously some time after (cf., Eckelbarger and Watling, 1995). Further, such reproductive linkages to the phytodetritus pulse could vary with trophic type, such that a greater degree of reproductive periodicity might be expected in surface deposit-feeders than in subsurface deposit-feeders due to their close association with typically more labile material deposited episodically to surface sediments (cf., Blake, 1993).

Labile organic material appears to be abundant and available year-round on the WAP shelf, particularly to particle-selective surface deposit-feeders (Mincks *et al.*, 2005a and b; Purinton, 2005). However, some deposit-feeders utilizing assimilatory selection for nutrient-rich particles (cf., Purinton, 2005) might experience a greater degree of seasonality in *high quality* organic material, and would thus be more likely to utilize seasonal resources to fuel vitellogenic processes. Nonetheless, benthic food resources appear to be relatively constant when compared to availability of particulate food in the water column (e.g., Chapter 2).

Reduced temporal variability in benthic food resources relative to those in the water column implies a lower risk of larval starvation in the benthos, relative to the water column. Thus, a persistent benthic food source should create selective pressure on benthos to invest more energy in the production of fewer, larger, non-feeding or direct-developing larvae. This increased parental investment could also take the form of brooding, and researchers have historically predicted high incidences of brooding and/or direct-developing (i.e., no morphologically distinct larval stage) species at high latitudes

(Thorson, 1950). However, more recently, patterns of seasonal spawning of planktonic larvae have been observed in a variety of taxa (e.g., Bosch *et al.*, 1987; McClintock and Pearse, 1987; Peck and Robinson, 1994). Nonetheless, many of these planktonic larvae are lecithotrophic (non-feeding), and are equipped by their parents to complete larval development and metamorphosis without reliance on planktonic food resources (e.g., Clarke, 1992; Pearse, 1994). Thus, production of non-feeding planktonic larvae does not necessarily require summer spawning, since larvae are not dependent on planktonic food sources. Rather, lecithotrophy could be an alternate method of increased parental investment utilizing predictably available benthic food resources (or a benthic "food bank" (Chapter 2; Smith *et al.*, 2005)).

Differential effects of food availability on planktotrophic larvae versus species with lecithotrophic or direct development could lead to variability in the timing of larval settlement and/or recruitment to the benthos. Planktotrophic larval stages would benefit from release into the water column shortly before or during the summer bloom, whereas non-feeding larvae could survive oligotrophic periods in the plankton, and could potentially be produced continuously throughout the year. Brooding species, in which embryos and/or larvae are maintained on or in the body of the parent, or in burrows or tubes, could exhibit either seasonal or non-seasonal reproductive patterns. Some brooders never release free-swimming larvae, and may be expected to lack reproductive periodicity entirely, assuming abundant resources for adults. However, some brooding species do release free-swimming larvae following the brood period (e.g., Peck and Robinson, 1994; Giangrande, 1997), and might spawn seasonally if their pelagic larvae are planktotrophic.

Despite any food-related variations in spawning behavior, food limitation for *newly settled benthic juveniles* may affect all developmental types equally. Thus, if food for *adults* is the dominant selective force in determining reproductive patterns, then lecithotrophic or direct-developing larval types would be expected, and seasonality of recruitment would be largely a function of the time required for larvae to complete development. Recruitment of such taxa could occur at low levels year-round. Alternatively, if food resources for *benthic juveniles* limit recruitment success, settlement might be expected in spring and summer in order to exploit summer phytodetritus deposition, regardless of whether the planktonic larval stage (i.e., developmental mode) was planktotrophic or lecithotrophic. Thus, timing of larval production of larvae in a seasonally variable environment is likely related to developmental mode. In contrast, timing of recruitment events, although influenced by the effect of larval type on the length of the development period, may be independent of reproductive strategy, and controlled by entirely different factors (e.g., post-settlement mortality; Olafsson *et al.*, 1994).

Is there seasonal recruitment on the WAP shelf?

About 75% of Annelid groups examined exhibited some degree of temporal variability in the abundance of juveniles (assuming no Type I errors; Harris, 1975; Sokal and Rohlf, 1995) (Table 1), most likely resulting from episodic recruitment events. Only three polychaete families—Paraonidae, Acrocirridae, and Ampharetidae—showed statistically significant evidence of temporal variability at multiple stations. These families were among the few in which distinct juvenile types (most likely species) could be distinguished in sufficient numbers for individual analysis, and seasonal patterns differed within families (Figs. 5-7). Further, patterns within families were not temporally coherent across stations. For paraonids and acrocirrids in particular, juveniles were fairly abundant year-round, with increases in abundance above "background" at particular time points.

Based on the variety of patterns in juvenile abundance, annelid taxa can be classified into three groups, exhibiting "seasonal", "marginally seasonal", and "non-seasonal" reproductive patterns (Fig. 17). "Seasonal" taxa may exploit temporally patchy resources (e.g., phytodetritus), with very low juvenile densities most of the year and large, rapid seasonal increases in abundance. "Marginally seasonal" patterns can best be characterized by moderately high and consistent levels of small individuals (juveniles), overlain by seasonally coherent recruitment peaks. The "non-seasonal" groups either exhibited essentially constant juvenile abundance year-round, or sporadic increases and decreases in juvenile abundance with little seasonal coherence. Three out of five megafaunal taxa also exhibited temporal variability in recruitment in particular locations (Table 2), including Bivalvia, Anthozoa, and Nemertea (Fig. 13). However, as will be discussed in detail below, these patterns seemed more closely linked to seasonal gametogenesis and spawning, rather than episodic recruitment events.

"Seasonal" recruitment in the macrofauna

"Seasonal" recruitment patterns were best represented by Acrocirridae (Fig. 5), Ampharetidae (Fig. 7), and Chrysopetalidae (Fig. 8). Acrocirrid sp. A peaked in abundance at Station B in Mar 2001, coincident with the large seasonal phytodetrital pulse, although juvenile abundance in the preceding few months (Jun - Oct 00) was also high. Acrocirrid sp. B, as well as both ampharetids, recruited in early spring (Oct 00) at particular locations.

Little is known about the reproductive patterns of these families, although ampharetids are thought to produce larvae with very short planktonic phases (3-5 d) (Hilbig, 2000), thus lacking obvious dependence on planktonic larval food resources. Consequently, any apparent reproductive periodicity should be driven by food availability for recruiting juveniles and/or reproductive adults. Glover *et al.* (2005) observed a large winter (Jun 00) peak in abundance of adult ampharetids at Station A. This group may reproduce on an annual cycle, reaching peak densities of reproductive adults following the summer phytodetritus pulse, and producing larvae with brief planktonic stages mostly settling in Sept/Oct, in anticipation of the onset of summer phytodetritus deposition. Nonetheless, this pattern is noisy, with substantial recruitment occurring at some stations throughout the year.

No data are available on the life histories of acrocirrids. However, L. Menot (personal communication) found high densities of juvenile acrocirrids, morphologically similar to those seen here, aggregated in localized patches of fertilized colonization trays in the deep Atlantic Ocean. Thus, this group, like the ampharetids, appears to be adept at taking advantage of episodic enrichment events.

While larval development in Chrysopetalidae is not well studied, chrysopetalids were the only polychaete family in this collection known to produce *long-lived* planktonic larvae (~30 d) in at least some species (Bhaud *et al.*, 1987; Rouse and Pleijel, 2001). Interestingly, chrysopetalids were rare among the larger polychaetes (>300), with only 50 mostly small (<10 setigers) individuals counted among the nearly 16,000 polychaetes collected (A. Glover *et al.*, unpublished data). This lack of larger individuals suggests adults are not a common component of the macrofauna on the WAP shelf.

"Marginally seasonal" and "non-seasonal" recruitment in the macrofauna

Members of the "marginally seasonal" group include Cirratulidae, Paraonidae, and Opheliid Type A (Figs. 6, 9 and 12). These taxa exhibited persistent background levels of small individuals in surface sediments, with periodic increases in abundance. Paraonids are believed to be direct developers, and there are no confirmed reports of planktonic larvae (Blake, 1996a; Giangrande, 1997), whereas cirratulids studied to date produce lecithotrophic larvae with a very brief (<10 d) planktonic stage (Bhaud et al., 1987; Petersen, 1999). At Stations B and C, these two groups (especially Paraonid sp. B) showed gradual increases in abundance throughout the spring and summer, in contrast to the sharp peaks at single sampling times observed in the "seasonal" taxa. However, at Station A, both groups exhibited more dramatic increases in abundance at a particular time point. Moderately high levels of juveniles present in sediments year-round suggest decoupling of recruitment from seasonal bloom dynamics. However, juvenile mortality and other controls may positively or negatively impact abundance of juveniles at different times throughout the year (see below).

Opheliid Type A was unique among all the polychaetes examined, and the "marginally seasonal" group in particular, with an early winter peak in abundance (Jun 00) at Station A. This opheliid strongly resembles a deep-sea species from the Porcupine Abyssal Plain (NE Atlantic) (Vanreusel *et al.*, 2001), which is thought to be an opportunistic species that maintains a small but stable pool of slowly developing juveniles, punctuated by episodic recruitment events in response to periodic phytodetritus pulses. Enrichment experiments using colonization trays have also shown opportunistic behavior in opheliids on lower-latitude continental shelves (Renaud *et al.*, 1999). The recruitment pulse we observed in Jun 00 was likely a similar response to sediment enrichment following the summer phytoplankton bloom.

Two groups labeled "non-seasonal" (Dorvilleidae, Syllidae) yielded statistically significant temporal variability in abundance only at Station C (Table 1). However, in contrast to the "marginal" group, examination of abundance data (Fig. 10) did not indicate any obvious seasonal patterns, and recruitment in these taxa thus appears uncoupled from seasonal bloom deposition. Like the cirratulids, dorvilleids are thought to produce larvae with a short non-feeding planktonic phase (<7 d) (Bhaud *et al.*, 1987; Hilbig, 1995b), whereas syllids are typically brooders (Kudenov and Harris, 1995). Dorvilleids and syllids are omnivorous or predatory groups with large jaws (Fauchald and Jumars, 1979), which may allow them to feed and reproduce essentially continuously.

The remaining "non-seasonal" macrofaunal taxa, including the oligochaetes and the polychaete groups Lumbrineridae, Spionidae, and Sabellidae, exhibited no statistically significant seasonal patterns at any location (Table 1; Fig. 11). Lumbrinerids and sabellids either brood or possess very short non-feeding larval stage (Bhaud *et al.*, 1987; Rouse and Fitzhugh, 1994; Hilbig, 1995a; Gambi *et al.*, 2000; Glover *et al.*, 2005). Similarly, oligochaetes do not produce planktonic larvae (Young *et al.*, 2002). Spionids represent somewhat of an anomaly in the "non-seasonal" group in that they are known for their diversity of *planktonic* larval forms (Blake, 1996b; Bhaud *et al.*, 1999; Blake and

Arnofsky, 1999). Spionid larvae were indeed found in FOODBANCS plankton samples (S. Mincks, unpublished observations), despite evidence of brooding in benthic adults (Glover *et al.*, 2005). However, spionids are the only polychaetes known to mix brooding strategy with production of planktotrophic larvae (Giangrande, 1997). Thus, it is not surprising that they fit into the non-seasonal category occupied by other brooding and demersally developing forms.

Based on life history data available in the literature (reviewed in Wilson, 1991; Giangrande, 1997), timing of seasonal recruitment pulses on the WAP shelf did not appear to be related to developmental mode in most taxa. Most of the abundant taxa are thought to produce larval stages with very limited or non-existent planktonic periods, including those that did exhibit some degree of temporal variability (or "seasonality"). However, the known brooders did consistently show non-seasonal abundance patterns. This high incidence of brooding, lecithotrophic, and direct developmental modes supports historical observations for high latitudes (e.g., Thorson, 1950); however, brooding is also the most common form of reproduction for polychaetes in general (Giangrande, 1997).

Other taxa not well represented in the small (<300 μm) size class (e.g., Spionidae) may possess planktonic larval stages that settle at sizes >300 μm (Blake and Watling, 1994; Bhaud *et al.*, 1999; Blake and Arnofsky, 1999). Additional analysis of larger individuals is thus required to determine recruitment patterns in these groups. Moreover, observations at the species level could uncover taxon-specific patterns obscured in family-level analyses. While generalizations could be made regarding seasonal patterns of recruitment, many gray areas exist. High developmental plasticity in the polychaetes (cf., Giangrande, 1997), with great diversity of reproductive mode even within families or genera, seems to have allowed a variety of strategies to arise in this seasonally productive environment.

Seasonality in the megafauna

Three megafaunal taxa exhibited statistically significant temporal variability in abundance of juveniles (>100 μm), including Anthozoa, Bivalvia, and Nemertea. Anthozoans at Station C showed a small recruitment peak in summer (Mar) 2000, and a much larger peak in abundance in summer 2001, whereas at Station A, abundances only increased substantially in summer 2001 (Table 2; Fig. 13). Bivalves also peaked in abundance in summer 2000 and 2001, with statistically significant seasonal differences only at Station A (Table 2; Fig. 13). Seasonal patterns in nemerteans differed somewhat from the other two groups, with peak abundance at Stations A and C in spring (Nov) 99, followed by a steady decline throughout the remainder of the sampling period (Table 2; Fig. 13).

Brooding is not widely reported in Anthozoa, which typically produce free-swimming lecithotrophic or planktotrophic planula larvae (reviewed in Young *et al.*, 2002, but see Waller *et al.*, 2005). Johnson *et al.* (2005) reported lecithotrophic (planktonic) development in the deep-water anemone *Bolocera kerguelensis* from the WAP shelf, with seasonal onset of vitellogenesis in *B. kerguelensis* linked to the summer bloom, and followed by a lengthy gametogenic period. Seasonal reproductive cycles have also been directly observed in deep-sea anemones (Van-Praet, 1990; Gage and Tyler, 1991). As predicted above, adult dependence on seasonal food sources appears to stimulate seasonal reproduction in lecithotrophic Antarctic anemones. Summer peaks in abundance of juvenile anthozoans (Fig. 13) suggest a lengthy larval period prior to settlement on WAP shelf sediments. This pattern represents a contrast to the year-round occurrence of planulae in shallow waters (<30 m) around Signy Island (maritime Antarctic) (Stanwell-Smith *et al.*, 1998), which suggests a *lack* of seasonality in reproductive behavior. However, selective pressures on reproductive strategy in the shallow-water, suspension feeder-dominated community likely differ from those in the deeper, soft-sediment shelf community.

Abundance patterns of juvenile nemerteans suggest a recruitment event in Nov 99 at one station (A) (Fig. 13). As invertebrate predators, adults of this taxon are not likely to be dependent on seasonally available phytodetrital food sources, whereas planktotrophic pilidium larvae would be. Reproductive studies of the abundant Antarctic nemertean *Parborlasia corrugatus* indicate developmental times of pilidium larvae on the order of 2 months (Peck, 1993), with peak abundance in the water column at Signy Island occurring in winter (Stanwell-Smith *et al.*, 1998). This pattern suggests spawning in late summer/early fall, followed by larval development under winter ice coverage, and spring recruitment. Surprisingly, larval abundance does not appear to be coincident with the summer phytoplankton bloom. Controlling mechanisms other than food availability, such as predation on planktonic larvae, may be at work.

Contrary to historical accounts (Thorson, 1950), planktonic larval stages are now known to be common in Antarctic bivalves. However, brooding is also unusually common in this group, often co-occurring with a brief planktonic stage (Arntz *et al.*, 1992; Hain and Arnaud, 1992; Peck and Robinson, 1994). Further, planktonic molluscan larvae occur seasonally at the height of the phytoplankton bloom in at least some

Antarctic locations (Shreeve and Peck, 1995; Stanwell-Smith *et al.*, 1998). Reproductive patterns in deep-sea bivalves have also been classified as "seasonal" (Tyler *et al.*, 1992; Gage, 1994). However, taxa with continuous gametogenesis have been reported, where lecithotrophic larvae are produced year-round even though size-frequency distributions suggest seasonally pulsed recruitment.

While juvenile bivalves could not be identified to the species level, the dominant bivalve in trawl collections at the FOODBANCS stations was *Limopsis marionensis* (C. Smith *et al.*, unpublished data), which is said to spawn pelagic lecithotrophic larvae (Hain and Arnaud, 1992). Thus, in the case of *L. marionensis*, we might expect either onset of vitellogenesis coincident with the spring bloom, or continuous reproduction. Recruitment data suggest essentially continuous settlement of bivalves in at least two WAP shelf locations (Stations B and C), with this pattern overlain by seasonal intensity of recruitment at Station A (Fig. 13). Lengthy developmental period and slow growth rates in Antarctic molluscs (e.g., Arntz *et al.*, 1992; Peck and Robinson, 1994; Peck, 1996; Ahn and Shim, 1998; Fraser *et al.*, 2002) may result in long-term presence of small individuals from a particular cohort in sediments. Length-frequency histograms (Fig. 16) suggest that "juveniles" counted here may include recruits from multiple years (cf., Gage, 1994). In addition, post-settlement controls may influence recruitment success at certain times of the year (e.g., Gage, 1994; Olafsson *et al.*, 1994), leading to a pattern of more or less constant juvenile abundance overlain by small seasonal increases above background levels.

Echinoderms were the most abundant megafauna on the WAP shelf, with particularly high numbers of two Elasipodid holothurians (*Protelpidia murrayi* and

Peniagone sp.) (Sumida *et al.*, 2005). However, limited numbers of juveniles appeared in megacore samples, making echinoderm recruitment patterns difficult to resolve. Seasonal reproduction has been reported in other Antarctic echinoderms (Bosch *et al.*, 1987; McClintock and Pearse, 1987; Stanwell-Smith and Clarke, 1998), although timing of spawning and settlement may vary.

Juvenile holothurians showed no statistically significant seasonal variability in abundance, but an increase was observed in one particular species (*Protelpidia murrayi*) in late winter months (Jun-Oct 00) (Fig. 14). This trend is supported by additional evidence from FOODBANCS sites, indicating initiation of seasonal gametogenic patterns linked to deposition of the summer phytodetritus pulse (Galley, 2003; Galley *et al.*, 2005). In addition, *P. murrayi* increased approximately 6-fold in abundance of from Nov 99 to Oct 00, apparently due to the presence of large numbers of small individuals in Oct with mean size nearly half that in Nov 99 (Sumida *et al.*, 2005). Inability to detect seasonal trends in juvenile abundance likely results from a lack of statistical power due to the relatively small numbers of individuals collected in megacores.

Seasonal spawning in winter has been detected in many deep-sea holothurians in areas with relatively predictable annual phytodetritus pulses (Tyler *et al.*, 1992). Antarctic and deep-sea invertebrates, and echinoderms in particular, exhibit long gametogenic periods and slow larval development, with limited evidence of linkages between planktonic larval abundance and availability of pelagic food resources even in "seasonally" reproducing taxa (Clarke, 1982; Pearse *et al.*, 1991; Peck and Robinson, 1994; Eckelbarger and Watling, 1995; Hoegh-Guldberg and Pearse, 1995; Galley, 2003). Indeed, a number of Antarctic studies indicate planktonic larvae are capable of surviving under relatively oligotrophic conditions, simply by utilizing bacteria and/or dissolved nutrients in seawater (Rivkin *et al.*, 1986; Olson *et al.*, 1987; Manahan, 1990; Pearse *et al.*, 1991; Peck, 1993; Marsh and Manahan, 1997). Thus, even feeding planktonic larvae can survive lengthy periods under winter ice cover, such that adults can take advantage of summer phytodetritus deposition without the negative effects of producing planktonic larvae in oligotrophic winter months.

Factors affecting recruitment success

Most of the seasonal increases in abundance of juvenile polychaetes observed in this study occurred in late winter/early spring (cf., Bowden, 2005)—not during or immediately following summer phytodetritus deposition—and was restricted to one or two locations. However, seasonal patterns in some other taxa also indicated recruitment in summer months. This temporally and spatially patchy response suggests that factors other than seasonal food availability (either for planktonic larvae or new recruits) must be at least partially responsible for recruitment success in macrofaunal polychaetes on the WAP shelf. In contrast, megafaunal taxa (Anthozoa, Bivalvia, Nemertea) showed some recruitment increases in summer months (Mar 00 and 01) (Fig. 13), coincident with peak phytodetritus deposition, suggesting tighter coupling to summer bloom events in selected taxa at certain locations. However, evidence for more slowly-reproducing species (cf., Eckelbarger and Watling, 1995) such as holothurians and anthozoans (e.g., Galley, 2003; Galley *et al.*, 2005; Johnson *et al.*, 2005) suggests this coupling might result from effects of food availability on gametogenesis, rather than on larvae or juveniles.

Some adult meio-, macro- and megafaunal detritivores appear to select for fresh phytodetritus when available in sediments (reviewed in Beaulieu, 2002; see also Suhr *et al.*, 2003). However, direct utilization of phytodetritus by larvae and/or juveniles has not been well documented (but see Qian and Chia, 1990). Size constraints have been predicted in developing deposit-feeders, such that greater need (and thus, greater selectivity) for highly labile food particles among juveniles constitutes a recruitment "bottleneck" (Jumars *et al.*, 1990). Periodic deposition of highly labile particles to otherwise food-poor habitats like the deep-sea may facilitate the transition of these juveniles to larger body sizes necessary to feed successfully on relatively organic-poor sediments (e.g., Hentschel, 1998 a & b; Rossi *et al.*, 2004). Thus, ontogenic shifts in feeding behavior and food resources of deposit feeders are highly likely, and we cannot assume *a priori* that recruitment would be non-seasonal in the presence of an apparently abundant adult food source (cf., Mincks *et al.*, 2005a).

Some deep-sea species with *non-seasonal* gametogenic patterns still appear to exhibit *seasonal* recruitment peaks coincident with phytodetritus pulses (Tyler et al., 1992). Such patterns support the idea of a food-related recruitment bottleneck, but do not rule out other controls on larval or juvenile success. Numerous factors may contribute to loss or mortality of planktonic larvae or benthic juveniles at various times of year, including predation in the plankton (e.g., by salps; see Loeb *et al.*, 1997), or on benthic juveniles.

Many classic exclusion studies (e.g., Grassle and Morse-Porteous, 1987) suggest mobile epibenthic predators can be important structuring forces in soft sediment habitats (reviewed in Olafsson *et al.*, 1994; Renaud *et al.*, 1999). Further, Ambrose and Renaud

(1997) suggested benthic predation-limited recruitment of macrofaunal polychaetes during seasonal phytodetritus deposition events, such that small increases in recruitment were observed between, rather than during, these food pulses. To date, no such studies have been conducted in Antarctic shelf sediments. However, the abundance of large, highly mobile epibenthic deposit-feeders capable of targeting patches of freshly deposited phytodetritus (see Beaulieu, 2002) suggest potentially serious impacts on benthic recruits, particularly during summer bloom periods. For example, pre-bloom peaks in abundance of the holothurian *Protelpidia murrayi* (Fig. 14), as well as the apparent migration of *Peniagone* sp. toward areas of high phytodetritus concentration (Sumida *et al.*, 2005), could serve to create predation pressure on newly settled juveniles at our stations. In addition, predation by nototheniid fishes on both infaunal and epifaunal polychaetes (Cantone *et al.*, 2000) could reduce numbers of new recruits.

In addition to predation effects, advective transport of larvae into (cf., Chrysopetalidae, see above) or out of the WAP shelf region could result from periodic intrusions of Antarctic Circumpolar Water onto the shelf (e.g., Hofmann *et al.*, 1996; Hofmann and Klinck, 1998). Affects of these intrusions on larval loss and/or supply might be particularly important nearest the shelf-break at Station C, where much temporal variability was detected, particularly in macrofaunal polychaetes (Table 1). Varying hydrographic regimes in Arctic polynya systems have been shown to influence community patterns in the underlying sediments, with ice-free areas showing relatively higher benthic biomass and faunal densities (Ambrose and Renaud, 1995; Piepenburg *et al.*, 1997). Hydrographic patterns in this region were found to significantly influence distributions of planktonic larvae, with maximum concentrations in localized gyres associated with particular topographic features (Clough *et al.*, 1997). Similar forces may be at work on the WAP shelf, particularly at Station A, which is located in a near-shore basin, and showed elevated deposition rates and sediment Chl-*a* concentrations likely due to topographic focusing (Smith and DeMaster, submitted; Mincks *et al.*, 2005a). Greater macrofaunal densities (e.g., Glover *et al.*, 2005) and multiple instances of seasonal recruitment could thus be related to small-scale hydrographic features at this location.

Implications for benthic-pelagic coupling on the WAP shelf

Evidence of seasonal gametogenic patterns in some WAP shelf megafauna (e.g., Galley, 2003; Galley *et al.*, 2005; Johnson *et al.*, 2005) suggests that a major influence of phytodetritus on life history parameters may operate at the level of adult reproductive success, rather than on larval or juvenile survival. Gametogenic patterns in macrofaunal polychaetes are not yet available for comparison, but abundance patterns of juvenile polychaetes suggest reproduction in the majority of taxa may be more or less continuous, with localized peaks in recruitment possibly related to seasonal detritus availability. These differences suggest that the nature of the coupling between benthic reproduction and the summer phytoplankton bloom may vary between macro- and megafauna.

Various studies have suggested that factors controlling community structure may differ between size classes of organisms. Megafaunal populations in and around an Arctic polynya showed no correlation between abundance of benthos and zones of elevated water column productivity, and thus no evidence of benthic-pelagic coupling (Piepenburg *et al.*, 2001). However, meio- and macrofaunal community patterns in the same study *did* reflect processes in the overlying waters, showing regional variations correlated with differing productivity regimes such as marginal ice zones and localized gyres (Piepenburg *et al.*, 1997; Piepenburg *et al.*, 2001). At the FOODBANCS sites, Sumida *et al.* (2005) found no correlation between phytodetritus cover and megafaunal abundance patterns. However, elevated *macrofaunal* abundances were recorded at Station A (Glover *et al.*, 2005), where sediment inventories of labile compounds (i.e., Chlorophyll-*a*, bioavailable amino acids) were also highest (Mincks *et al.*, 2005a). This pattern suggests a possible linkage between macrofaunal abundance and/or recruitment and organic enrichments, despite the lack of such correlations for megafaunal abundance at the same locations.

Taxa known to exhibit "enrichment opportunist" strategies in other areas, such as capitellid polychaetes and ophiuroids (Grassle and Morse-Porteous, 1987; Tyler *et al.*, 1992; Renaud *et al.*, 1999), did not show significant evidence of recruitment (this study), or numerical dominance of assemblages at the FOODBANCS stations (Glover *et al.*, 2005; Sumida *et al.*, 2005). Instead, the most abundant megafauna included long-lived, slow-growing taxa such as the holothurians, and brooding species such as the echinoids *Amphineustes* spp. and *Ctenocidaris perrieri*. In addition, macrofaunal polychaetes assemblages were overwhelmingly dominated by a brooding spionid species, as well as other taxa exhibiting reproductive strategies that involve high levels of parental investment (i.e., brooding, lecithotrophic larvae) and minimal seasonality. Further, recruitment patterns seemed to be dominated by continuous presence of small juveniles, with occasional increases in some taxa at particular locations and times. These patterns are not consistent with a regional, community-wide dependence on summer bloom detritus for recruitment success. The WAP shelf thus appears to experience year-round availability of relatively labile detritivore food sources (i.e., a sediment “food bank”), overlain by brief but predictable inputs of phytodetritus, rather than a nutrient-poor system with organisms dependent on rapid response to seasonally ephemeral food sources.

Table 1. Seasonal variability in abundance of juvenile Annelida at each station. Adult feeding mode (based on Fauchald and Jumars, 1979) is abbreviated as follows: OMNI = omnivore; SDF = surface deposit-feeder; SSDF = subsurface deposit-feeder. Possible reproductive modes are abbreviated as follows: P = feeding or non-feeding planktonic stage; B = brooder; D = direct development. Statistically significant seasonal differences (One-way ANOVA) are indicated for each station by * (*: $p < 0.10$; **: $p < 0.05$; ***: $p < 0.001$; ns = not significant), followed by the month(s) in which peaks in abundance were observed.

Family	Feeding Mode	Reprod. Mode	N	Station A	Station B	Station C
Oligochaeta	SSDF		86	ns	ns	ns
Polychaeta			2581	**/Oct	ns	***/Oct
Acrocirridae						
Sp. A	SDF	?	92	ns	*/Mar 01	ns
Sp. B	SDF	?	104	**/Oct	ns	*/Oct
Ampharetidae	SDF	P	194	**/Oct	ns	***/Oct
Sp. A	SDF	P	70	**/Oct	ns	ns
Sp. B	SDF	P	113	ns	ns	***/Oct
Chrysopetalidae	OMNI	P	137	ns	ns	**/Oct
Cirratulidae	SDF	P,D	157	ns	ns	***/Oct
Dorvilleidae	OMNI	P	36	ns	ns	**/Mar 00, Oct
Lumbrineridae	OMNI	P	54	ns	ns	ns
Opheliidae						
Type A	SSDF	P	180	**/Jun	ns	ns
Paraonidae	SSDF	P,D	815	***/Mar 00	ns	***/Jun,Oct,Mar
Sp. A	SSDF	P,D	39	ns	ns	ns
Sp. B	SSDF	P,D	545	**/Mar 00	*/Mar 01	***/Jun 00-Mar 01
Sabellidae	SDF	B	116	ns	ns	ns
Spionidae	SDF	P,B	75	ns	ns	ns
Syllidae	OMNI	P,B	491	ns	ns	**/Mar, Oct

Table 2. Seasonal variability in abundance of juvenile megafauna at each station. Feeding modes include Predators/Scavengers (P/S), Surface Deposit-Feeders (SDF) and Subsurface Deposit-Feeders (SSDF). Statistically significant seasonal differences(One-way ANOVA) are indicated for each station by * (*: $p = 0.10$; **: $p = 0.05$; ***: $p = 0.001$; ns = not significant), followed by the month(s) in which peak abundances were observed.

Taxon	Feeding Mode	N	Station A	Station B	Station C
Anthozoa	P/S	77	**/Mar 01	ns	***/Mar 00, 01
Bivalvia	SSDF	554	**/Mar 00, 01	ns	ns
Holothuroidea					
Total	various	160	ns	ns	ns
Protelpidia murrayi	SDF	63	ns	ns	ns
Peniagone sp.	SDF	40	ns	ns	ns
Nemertea	P/S	112	**/Nov 99	ns	*/Nov 99
Sipuncula	SDF	124	ns	ns	ns

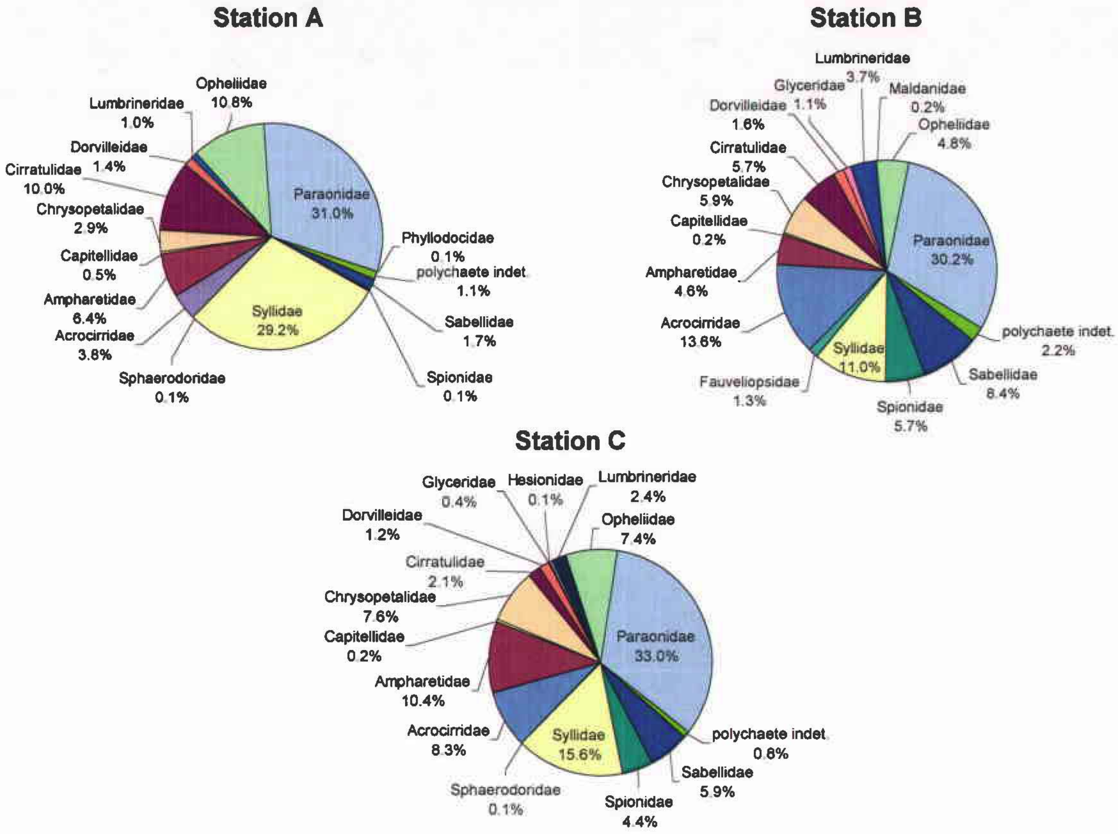


Fig. 1. Composition of polychaete taxa (families; 100-300 μm) at each station.

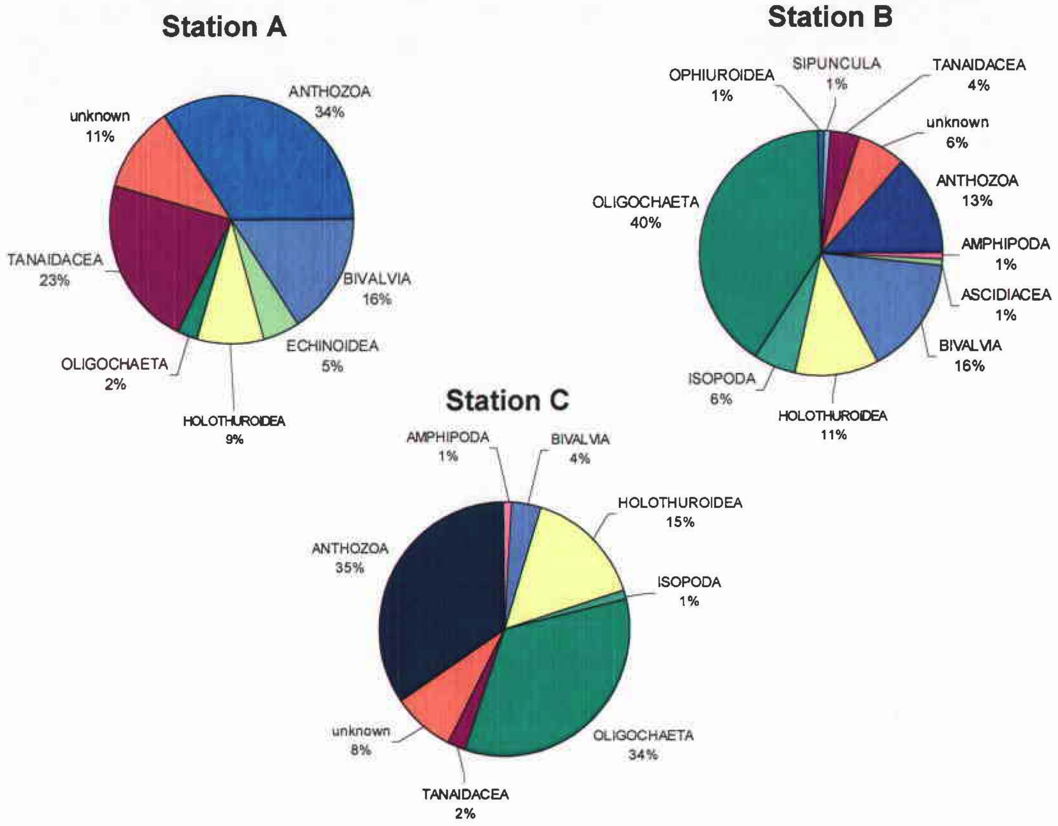


Fig. 2. Composition of the non-polychaete taxa (100-300 μm) at each station.

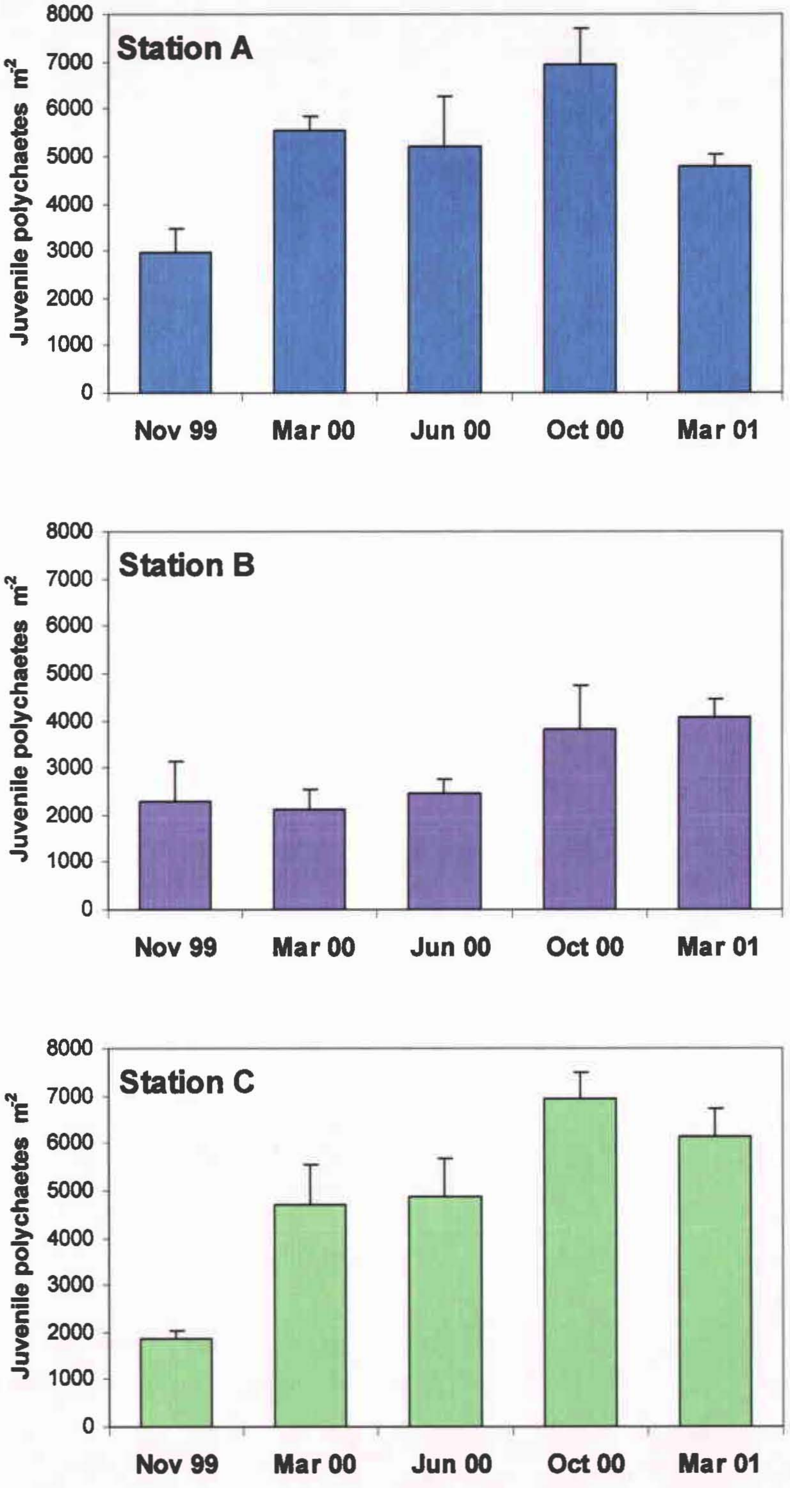


Fig. 3. Abundance (individuals m^{-2}) of juvenile polychaetes (100-300 μm) at each station (0-5 cm depth).

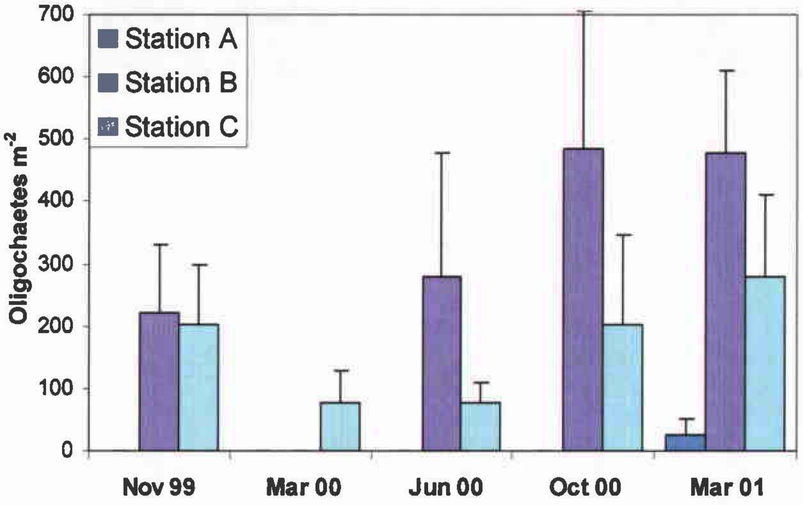


Fig. 4. Abundance (individuals m^{-2}) of juvenile oligochaetes (100-300 µm) at all stations (0-5 cm depth).

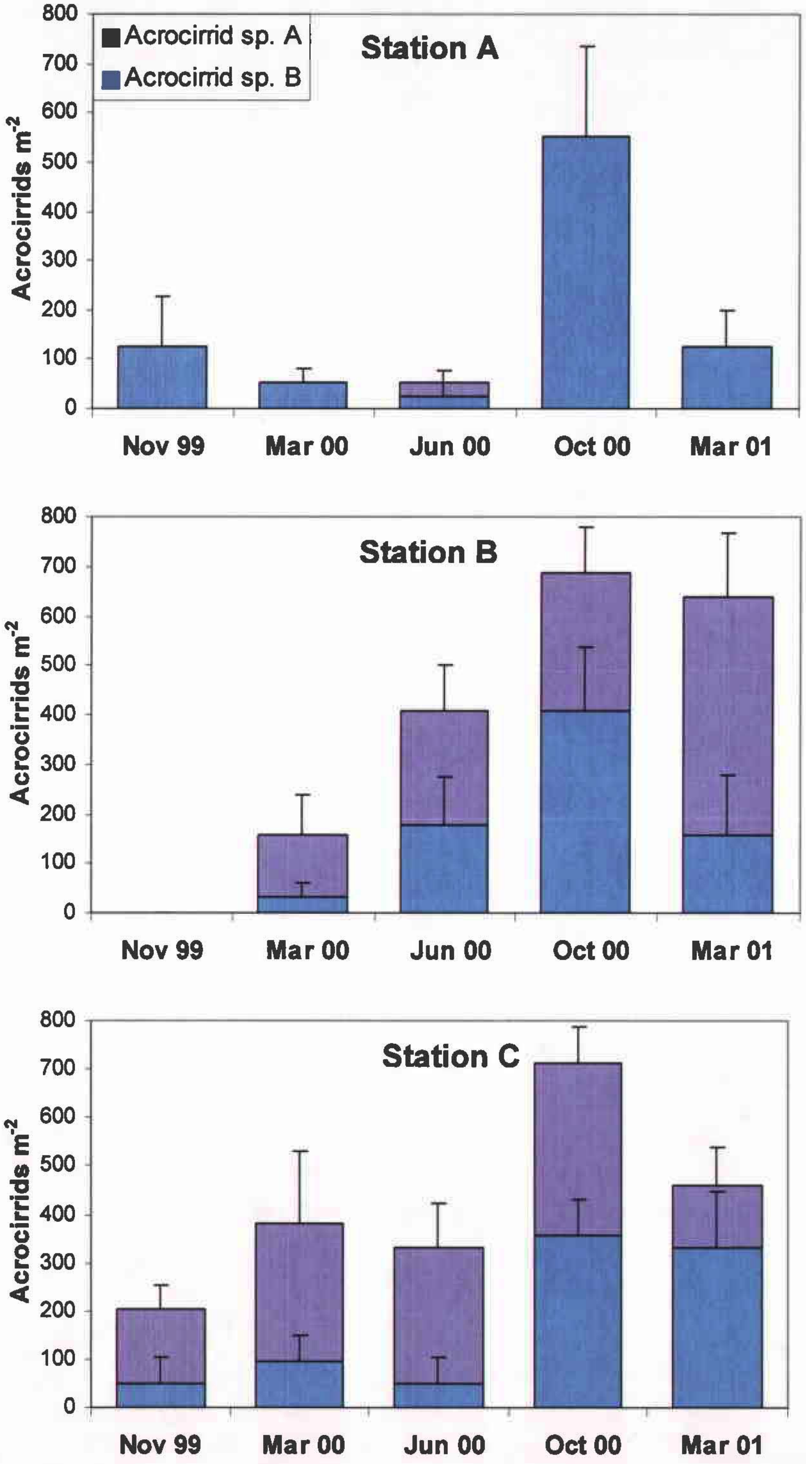


Fig. 5. Abundance (individuals m^{-2}) of Acrocirrids sp. A and B (100-300 μm) at Station A (top panel), Station B (middle panel), and Station C (bottom panel) (0-5 cm depth).

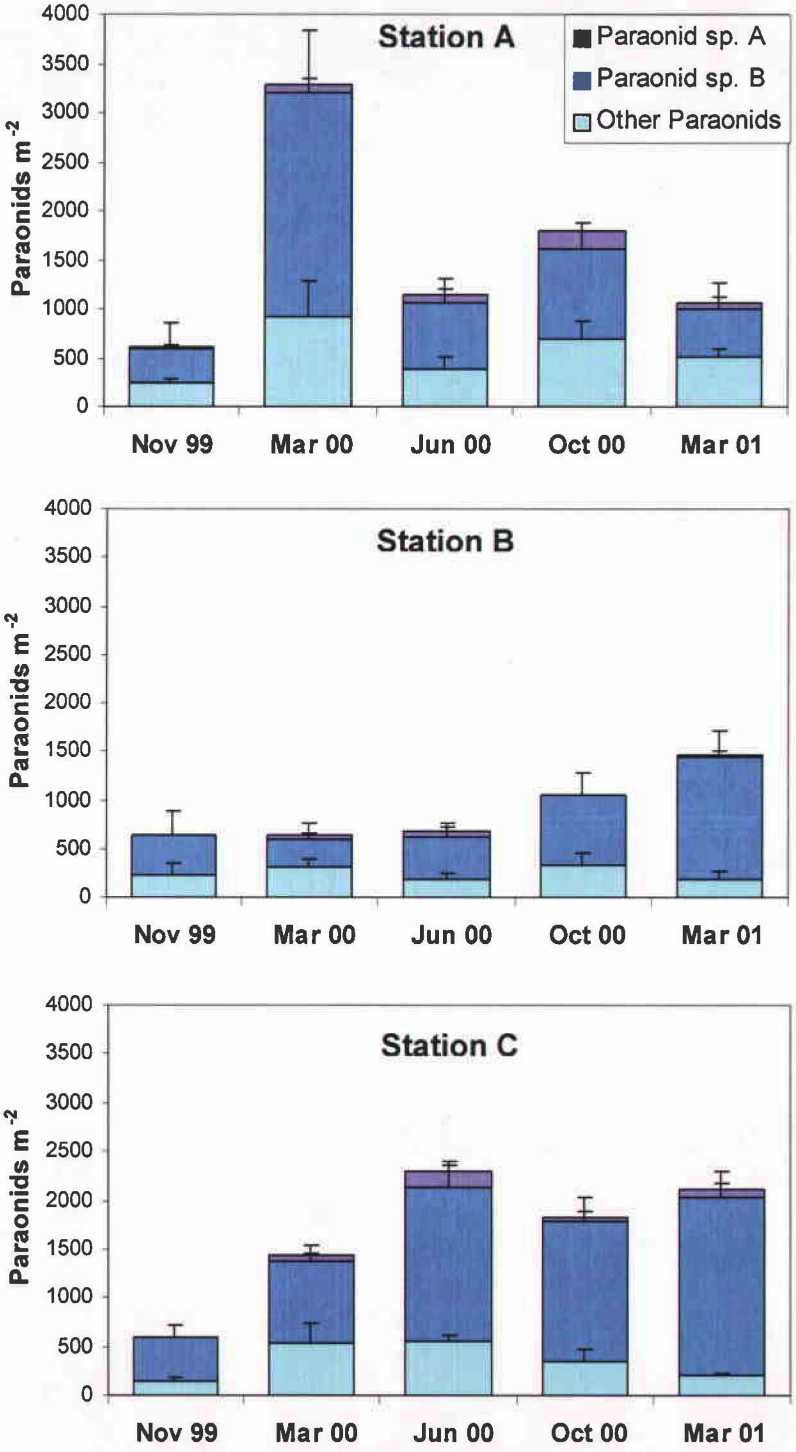


Fig. 6. Abundance (individuals m^{-2}) of Paraonid spp. A and B and other paranoids (100-300 μm) at Station A (top panel), Station B (middle panel), and Station C (bottom panel) (0-5 cm depth).

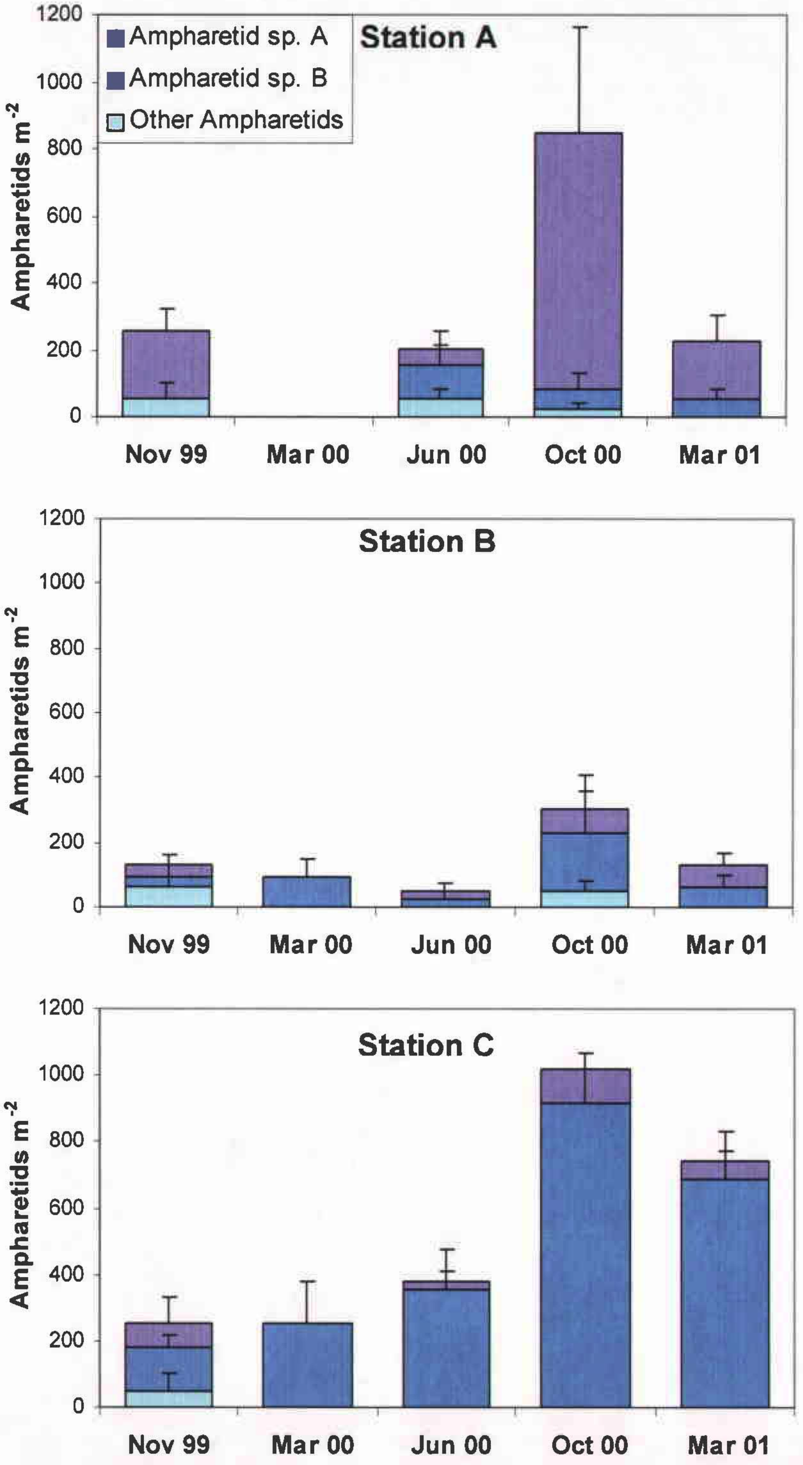


Fig. 7. Abundance (individuals m^{-2}) of Ampharetid sp. A and B and other ampharetids (100-300 μm) at Station A (top panel), Station B (middle panel), and Station C (bottom panel) (0-5 cm depth).

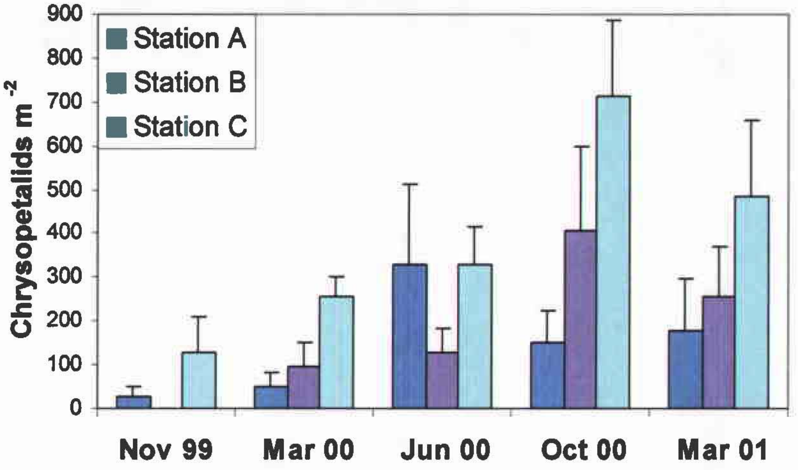


Fig. 8. Abundance (individuals m^{-2}) of Chrysopetalidae (100-300 μm) at all stations (0-5 cm depth).

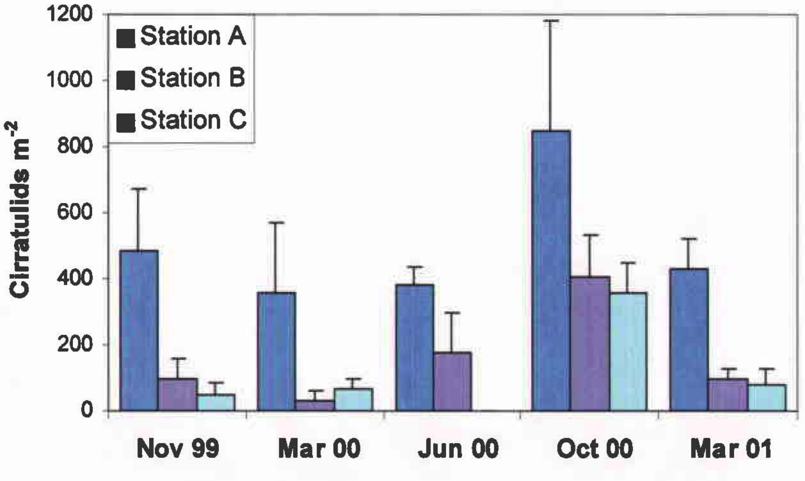
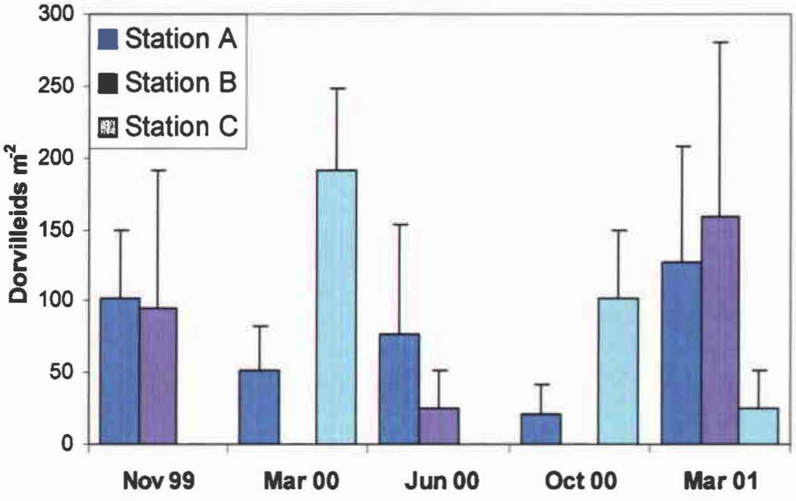


Fig. 9. Abundance (individuals m^{-2}) of Cirratulidae (100-300 μm) at all stations (0-5 cm depth).



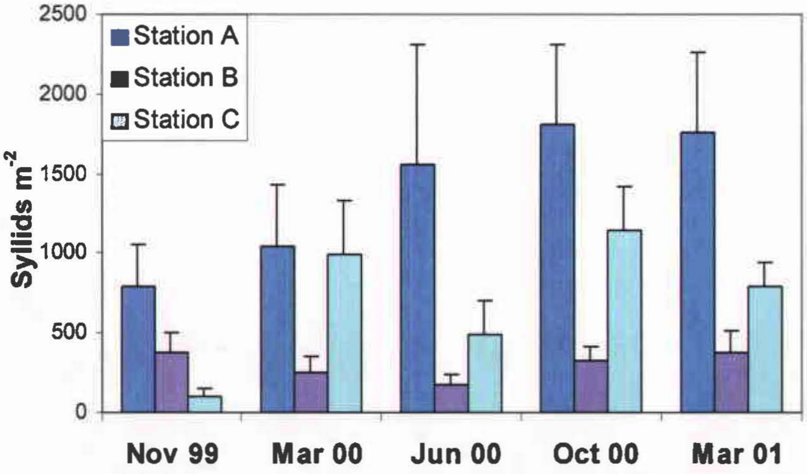


Fig. 10. Abundance (individuals m^{-2}) of "non-seasonal" polychaete taxa Dorvilleidae (top panel) and Syllidae (bottom panel) (100-300 μm; 0-5 cm depth). Patterns were statistically significant only at Station C.

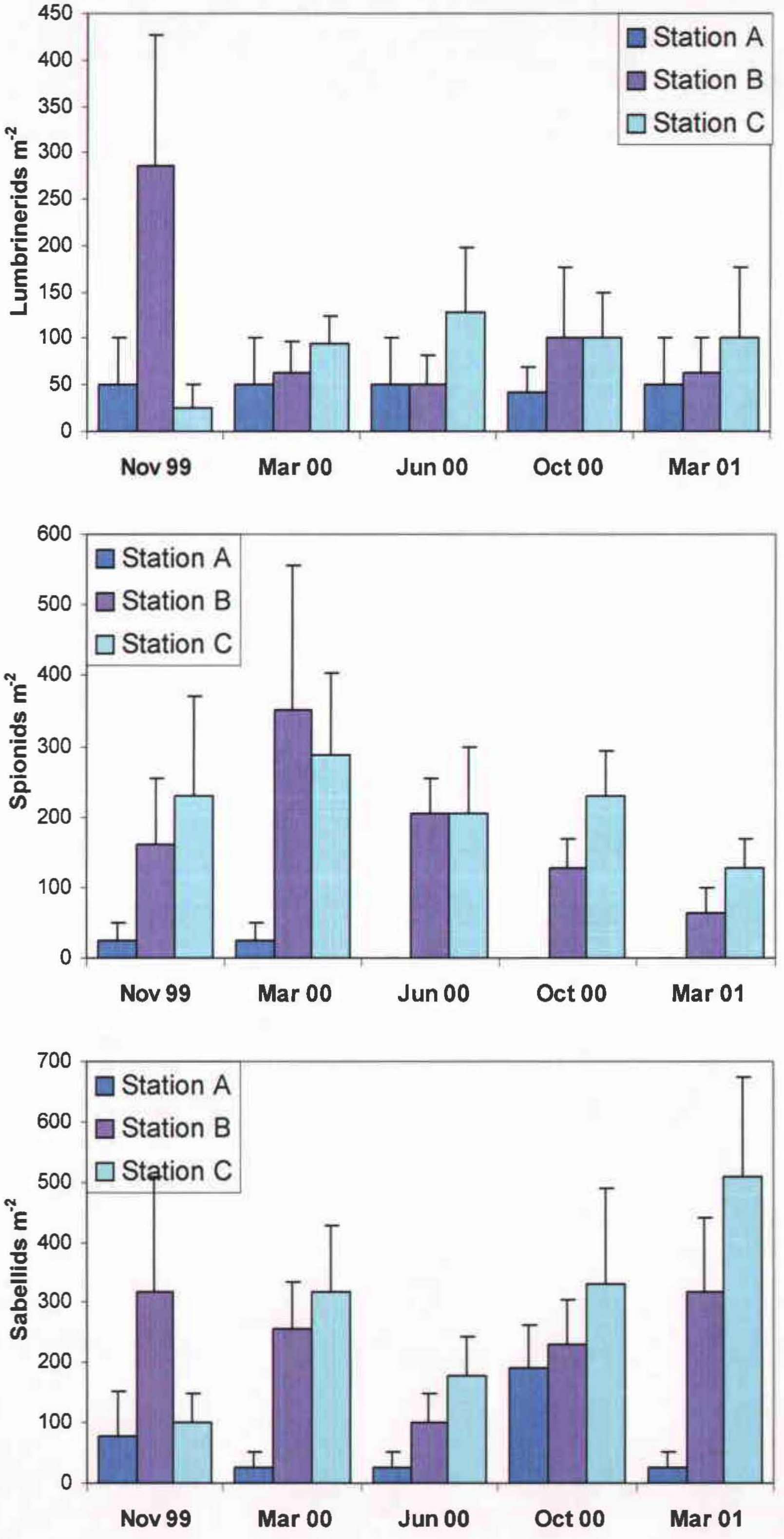


Fig. 11. Abundance (individuals m^{-2}) of "non-seasonal" polychaetes (100-300 μm) at all stations: Lumbrineridae (top), Spionidae (center), and Sabellidae (bottom) (0-5 cm depth).

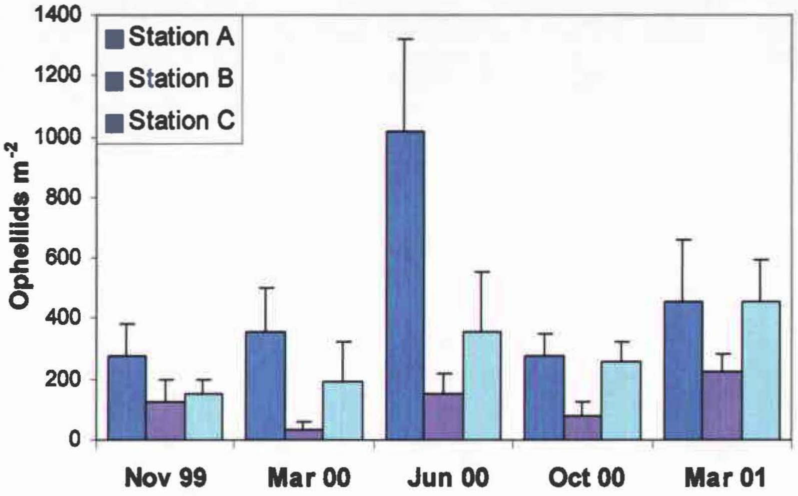


Fig. 12. Abundance (individuals m^{-2}) of Opheliid Type A (100-300 μm) at all stations (0-5 cm depth).

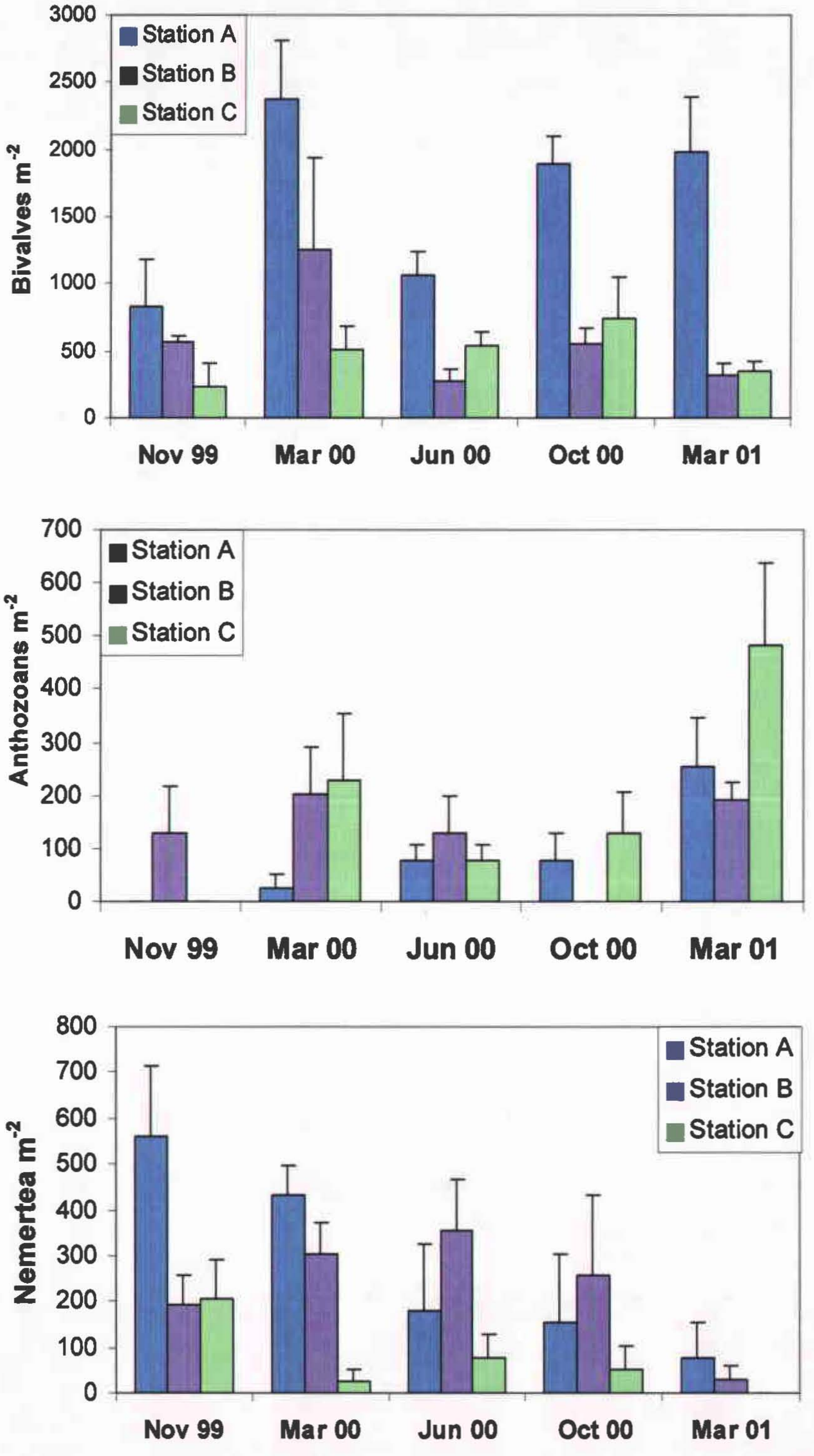


Fig. 13. Abundance (individuals m^{-2}) of juvenile megafauna (>100 μm) in the top 5 cm of sediment. Top: Bivalvia, Center: Anthozoa, Bottom: Nemertea.

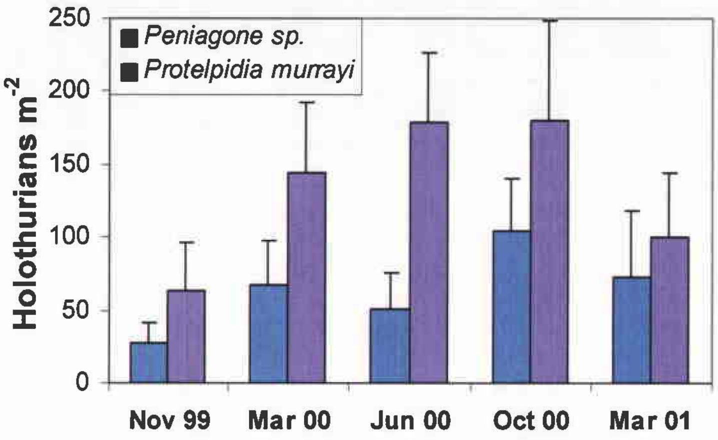


Fig. 14. Abundance (individuals m^{-2}; average of Stations A, B, and C) for the holothurians *Peniagone* sp. and *Protelpidia murrayi* (>100 µm) in the top 5 cm of sediment.

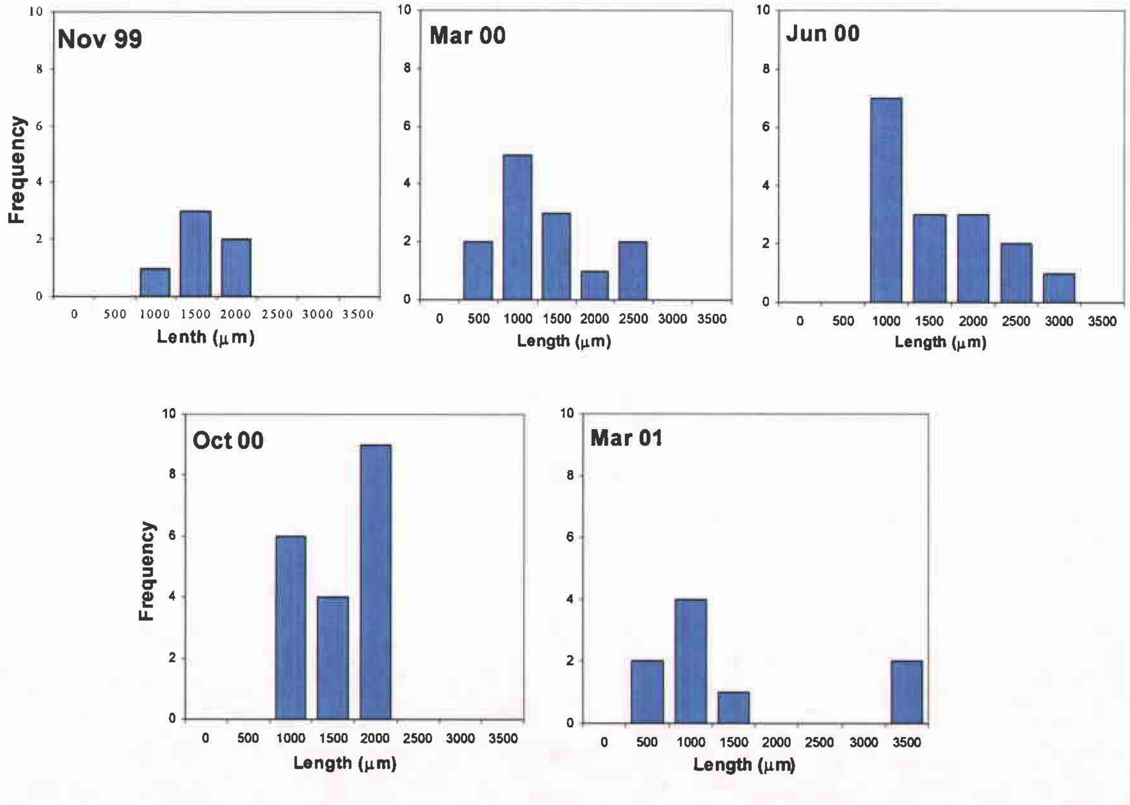


Fig. 15. Length-frequency histograms for *Protelpidia murrayi* (>100 µm; n = 63) at all stations.

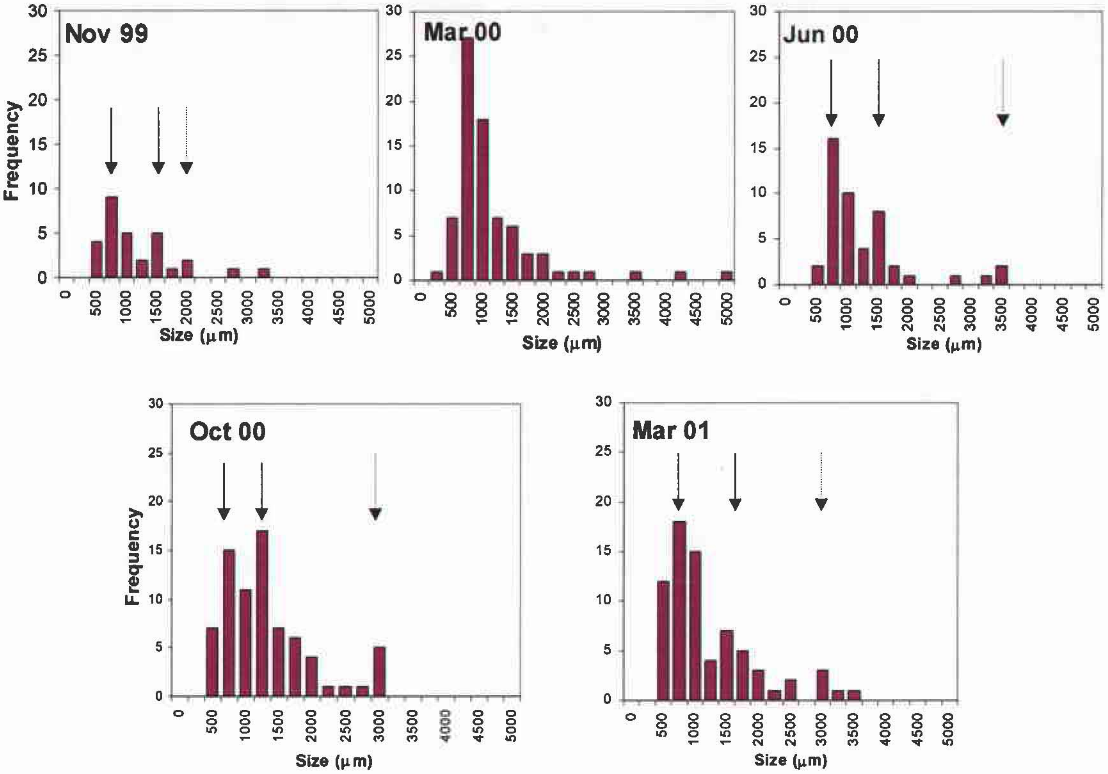
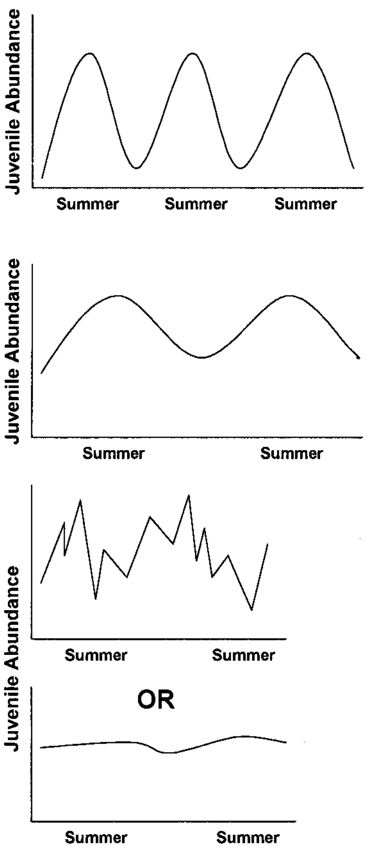


Fig. 16. Length-frequency histograms for Bivalvia (>100 μm) at Station A (n = 302). Solid arrows indicate two distinct cohorts at a given time point. Dashed arrows indicate a possible third cohort.



"Seasonal"

- Distinct cohorts settling synchronously.
- Spatial and temporal coherence in recruitment patterns.
- Dramatic seasonal boom/bust abundance patterns.
- Appear to be utilizing seasonally available resources.
- **e.g., Ampharetids, Acrocirrids**

"Marginally Seasonal"

- Constant, relatively high "background" population of juveniles, overlain by periodic (possibly *localized*) recruitment events.
- May be reproducing continuously, but taking advantage of temporally patchy resources when available OR subjected to recruitment "bottlenecks".
- May have long developmental times, such that multiple cohorts are present in the "juvenile" size classes for multiple years.
- **e.g., Cirratulids, Paraonids, Bivalves**

"Non-Seasonal"

- Sporadic highs and lows in abundance of juveniles.

OR

- Constant abundance of juveniles, possibly with recruitment peaks widely spaced in time.
- Probably not directly influenced by seasonal food resources (i.e., may be predatory).
- Likely to be brooders or produce lecithotrophic larvae.
- **e.g., Dorvilleids, Syllids, Sabellids, Oligochaetes, Nemerteans?**

Fig. 17. Conceptual model of seasonal recruitment patterns in benthic macro- and megafauna.

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CHAPTER 5. CONCLUSIONS

High latitude ecosystems have become increasingly important regions for study as evidence of climatic warming mounts (e.g., Clarke and Harris, 2003; Smith *et al.*, 2003), and changes in physical conditions such as ice-coverage (Fetterer and Knowles, 2002; Smith *et al.*, 2003) become obvious. Because polar marine organisms are uniquely adapted to their low-temperature environment—in some cases able to withstand only narrow fluctuations in environmental temperature (e.g., Hardewig *et al.*, 1999; Pörtner *et al.*, 1999; van Dijk *et al.*, 1999)—global warming might be expected to impact polar ecosystems sooner, and with more severity, than any other ecosystems on earth. Thus, these ecosystems provide a valuable opportunity to monitor the impacts of warming as they unfold.

The primary objective of the research presented here was to contribute to the understanding of high-latitude benthic ecosystem functioning, to better recognize and predict the impacts of climate change. Water column process and dynamics of the pelagic and sea ice-associated communities along the West Antarctic Peninsula have been under observation for more than a decade (e.g., Baker *et al.*, 1996; Karl *et al.*, 1996; Smith *et al.*, 2001). However, little was known about the nature and strength of the coupling between pelagic process and carbon storage or community dynamics in the underlying sediments. I sought to evaluate, within the framework of the FOODBANCS (FOOD for Benthos on the ANtarctic Continental Shelf) program, the transfer of seasonal primary production to sediments, and the availability of summer bloom-derived detritus to benthos. Evidence of long-term storage of bioavailable material (i.e., a sediment "food bank"; **Chapter 2**), suggests benthos experience less temporal variability in food resources than do pelagic organisms. Analysis of trophic relationships among benthic fauna confirmed that the summer phytodetritus pulse is utilized by benthos, and that relatively labile material is available to particle-selective detritivores year-round (**Chapter 3**). Finally, the existence of a persistent detritivore food source appeared to influence reproductive behavior in many benthic taxa, such that recruitment of juveniles to the benthos occurs essentially continuously throughout the year, with localized peaks in recruitment possibly related to summer phytodetritus deposition (**Chapter 4**).

A sediment "food bank" on the Antarctic continental shelf

Despite the evidence of dramatic seasonal and interannual variability in water column processes and vertical particulate fluxes on the Antarctic continental shelf, pools of bioavailable organic matter in sediments remain relatively stable, with minor temporal fluctuations limited to the upper few cm (**Chapter 2**; Mincks *et al.*, 2005). Further, labile components of the sediment organic pool (e.g., chloropigments, bioavailable amino acids) are not only present year-round, but are abundant relative to other marine sediments (e.g., Cahoon *et al.*, 1994; Smith *et al.*, 1996; Fabiano and Danovaro, 1998; Dauwe *et al.*, 1999; Dell'Anno *et al.*, 2000; Danovaro *et al.*, 2001; Demopoulos *et al.*, 2003). Diagenetic modeling suggested that this labile material degrades relatively slowly at FOODBANCS stations, on the order of months to years (Table 2.3).

Abundant labile organic material persisting for months in WAP shelf sediments would seem to suggest that microbial reworking of seasonally deposited phytodetritus is somehow limited. However, sediment microbial biomass remains high year-round (Figs.

2.8 and 2.9), and sediment community respiration rates at FOODBANCS sites and elsewhere on the Antarctic shelf vary little with season, appearing broadly in balance with vertical particulate carbon flux (Nedwell *et al.*, 1993; Thomas *et al.*, 2005).

These patterns led to the hypothesis, laid out in **Chapter 2**, that the consistently low bottom water temperatures may limit remineralization of sediment organic material in Antarctic shelf sediments, such that higher levels of organic substrate are required to stimulate increased microbial enzymatic activity relative to temperate waters (Fig. 2.10) (cf., Pomeroy and Deibel, 1986; Wiebe *et al.*, 1993). This "temperature-substrate limitation" of microbial metabolism may have allowed background levels of organic material to build up to the relatively high levels observed in WAP shelf sediments, forming a sediment "food bank" that sustains benthic detritivores throughout low-flux seasons (i.e., winter) or years.

The existence of a persistent detritivore food source in WAP shelf sediments likely affects most aspects of benthic community dynamics in this region, causing benthic processes to exhibit inertia in response to extreme seasonal and interannual variability in primary production in overlying waters (reviewed in Gutt, 2000; Smith *et al.*, 2005). Experimental evidence of the effects of temperature increases on microbial hydrolytic enzyme efficiency at very low temperatures (e.g., Arnosti *et al.*, 1998; Arnosti and Jorgensen, 2003) indicates that warming of Antarctic shelf bottom waters by even a few degrees could significantly enhance the efficiency of microbial remineralization, drawing down these background levels of labile organic material in sediments. Thus, if current warming trends continue (cf., Smith *et al.*, 2003), the sizeable "food bank" currently available to benthic detritivores could be substantially depleted.

Role of the sediment "food bank" in benthic ecological processes

Many previous studies have emphasized the intense seasonality of the Antarctic marine environment as a key structuring force in benthic communities (e.g., Peck *et al.*, 1987; Clarke, 1988; Pearse *et al.*, 1991; Arntz *et al.*, 1994; Clarke and Leakey, 1996; Brockington *et al.*, 2001; Fraser *et al.*, 2002). Indeed, seasonal and/or interannual variability in pelagic primary production might be expected to impact hard-substrate intertidal or shallow subtidal areas and suspension feeder-dominated communities more heavily (e.g., Barnes and Clarke, 1995; Orejas *et al.*, 2000). However, direct coupling between water column processes and key benthic parameters (e.g., biomass, diversity, sediment organic matter) in the vast deeper-water, soft-sediment regions of the Antarctic shelf often appear weak (reviewed in Arntz *et al.*, 1994; Gutt, 2000; Smith *et al.*, 2005). To some degree, these "missing links" may be the result of incomplete knowledge of the biology of many Antarctic fauna (e.g., Gutt, 2000). However, evidence from the FOODBANCS program has begun to suggest that many such benthic-pelagic linkages may simply be weak, or dominated by slow response times.

FOODBANCS collaborators have investigated various aspects of the biology of WAP shelf benthos (e.g., reproductive patterns, deposit feeding, community structure), in an attempt to address the role of benthic-pelagic coupling in governing benthic ecological processes (Wigham *et al.*, in prep.; McClintic, 2002; Galley, 2003; Galley *et al.*, 2005; Glover *et al.*, 2005; Johnson *et al.*, 2005; Purinton, 2005; Sumida *et al.*, 2005; Waller *et al.*, 2005). Significant aspects of benthic ecology examined here included utilization of summer bloom detritus by detritivores and trophic relationships among benthic megafauna (**Chapter 3**), as well as linkages between seasonal phytodetritus deposition and recruitment to the benthos (**Chapter 4**). The sum total of all the FOODBANCS results substantiates the existence of a detritivore "food bank", and the resultant stabilization of temporal variability in benthic food resources. Further, aspects of benthic biology studied thus far appear to be less influenced by seasonal food availability than has been suggested for intertidal or shallow subtidal organisms.

Feeding on the "food bank": Trophic relationships among benthic megafauna

Many studies suggest episodic inputs of surface-derived phytoplankton detritus quickly stimulate feeding by detritivores (e.g., Gooday and Turley, 1990; Beaulieu, 2002; Suhr et al., 2003). In order to determine whether summer bloom-derived phytodetritus is a key component of the benthic food web on the WAP shelf, stable isotope analyses were conducted on trophic end-members (e.g., sediments, phytodetritus, sinking particulates) and major benthic megafaunal organisms (**Chapter 3**). If detritivores rely heavily on summer bloom-derived detritus as a food source, then seasonal changes in stable isotope values of food sources should be reflected in tissues, and organisms may be expected to exhibit seasonality in biological processes such as growth and reproduction. However, evidence of a sediment food bank led to predictions that seasonal changes in stable isotopic composition of the benthic fauna would be minimal, despite extreme annual/interannual variability in particulate organic matter fluxes.

While broad ranges in stable isotope values were detected in plankton at our study sites, values in surface sediments remained relatively constant throughout the sampling period (Fig. 3.2). Further, stable isotope evidence indicated that fresh algal material was deposited rapidly to the seafloor, such that minimal degradation occurred in the water column. The year-round similarity in isotopic composition of benthic organisms to that of surface sediments and phytodetritus (particularly in $\delta^{15}N$) suggested recently deposited material was being incorporated into the benthic food web throughout much of the year. In particular, particle-selective surface deposit-feeders such as spionid polychaetes (Fig. 3.9) and holothurians (Fig. 3.8a) maintained temporally consistent carbon isotopic values in their body tissues, indicating labile material could be obtained from surface sediments even in low-productivity periods (i.e., winter). Thus, detritivore food resources appeared to have substantial "inertia" (cf., Smith *et al.*, 2005), dampening the effects of the extreme temporal variability in overlying waters.

Despite the relatively narrow range of values in sediments and sediment-trap material, a wide range in $\delta^{13}C$ values of benthic detritivores was observed, suggesting organisms were utilizing particular components of the labile organic pool in their feeding behavior (Fig. 3.5). In addition, a second subset of organisms appeared to derive nutrition from planktonic food sources (e.g., the anemone *Isosycionis alba*). The ability to select particular components of the detritus pool may result in trophic niche separation among organisms with similar feeding modes and overlapping food resources (cf., Jacob *et al.*, 2003; Lovvorn *et al.*, 2005).

Seasonal patterns of recruitment to the benthos

Many previous studies have sought to draw correlations between seasonality in food resources and reproductive patterns in Antarctic shelf benthos (e.g., Thorson, 1950; Picken, 1980; Pearse *et al.*, 1991; Clarke, 1992; Pearse, 1994). Most of these studies conclude that developmental modes are strongly dictated by the seasonality of particulate material in the water column, such that *larval* food availability is the dominant selective force creating patterns of more frequent lecithotrophic, direct-developing, and brooded larvae in Antarctic taxa. Recruitment studies, in contrast, are few and far between in Antarctic waters, probably in no small part due to the logistical difficulty in carrying out high-resolution time-series studies in this remote location (but see Stanwell-Smith and Barnes, 1997; Barnes, 2000). By examining the temporal variability in abundance of juvenile macro- and megafauna over 1.5 annual cycles, I was able to observe temporal patterns in recruitment to the WAP shelf benthos (**Chapter 4**). The presence of a persistent food source for adult detritivores, combined with relatively ephemeral food resources for pelagic larvae, was expected to result in a tendency toward increased parental investment (i.e., brooding and lecithotrophy), and minimal linkages to the summer bloom in larval production and recruitment.

The majority of taxa examined (mostly macrofaunal polychaetes) exhibited some evidence of temporal variability in abundance of juveniles present in sediments (Table 4.1). However, these patterns were largely confined to particular locations, and did not exhibit much spatial or temporal coherence across the FOODBANCS study sites. The most common pattern observed was one of relatively constant, moderately high abundances of small juveniles in sediments throughout the year, punctuated by localized peaks assumed to be recruitment events (cf., Paraonid sp. B, Fig. 4.6). Thus, seasonal enhancement of recruitment success may be related to a variety of factors in addition to seasonal food availability, including food-related recruitment bottlenecks (cf., Jumars *et al.*, 1990; Hentschel, 1998), post-settlement predation (Ólafsson *et al.*, 1994), or advective transport of larvae in to or out of the local environment. Further, evidence from gametogenic studies on major WAP shelf megafauna (e.g., Galley, 2003; Johnson *et al.*, 2005) suggest any seasonal recruitment patterns in these taxa is more likely the result of linkages between the summer bloom and *production* of non-feeding pelagic larvae, rather than seasonal settlement and metamorphosis. Thus, recruitment patterns were not consistent with a regional, community-wide dependence on summer bloom detritus for recruitment success. Rather, the presence of the sediment "food bank" appeared to allow year-round recruitment in most taxa.

While the abundance of brooding and lecithotrophic forms in Antarctic waters has historically been attributed to short and unpredictable availability of surface production, recent studies have suggested that the radiation of brooding taxa could result from evolutionary rather than environmental success (Poulin and Feral, 1996; Poulin *et al.*, 2002). Specifically, these studies indicate that brooding and lecithotrophy arose in Antarctic fauna prior to the initial glaciation of the continent (~38 mya), and that the subsequent decrease in primary productivity beneath thick, multi-year ice sheets led to the elimination of most planktotrophic species while allowing brooders to survive. Brooders and lecithotrophic species reproduce via the production of a smaller number of large, yolky eggs, as opposed to planktotrophic species that produce many smaller eggs. The production of a few large eggs has long been thought to be energetically less costly (Vance, 1973; reviewed in Emlet *et al.*, 1987), and has been considered an adaptive strategy of species in nutrient-poor environments (e.g., Picken, 1980). The implied linkage between food availability in the sediments and successful production of larvae suggests that decreasing the size of the sediment "food bank" (e.g., by warming of sediments) could have profound implications for brooding and lecithotrophic forms.

Further, to the extent that summer bloom detritus helps to enhance recruitment success, perhaps by alleviating a food-related recruitment bottleneck (cf., Jumars *et al.*, 1990), warming effects on the "food bank" could severely impact recruitment in benthic taxa.

Implications for Antarctic climate change research

Numerous modeling studies have indicated that high-latitude oceans played an important role in lowering atmospheric CO_2 levels during the last glacial maximum, through enhanced primary production in surface waters and/or variations in vertical mixing of nutrient-rich deep water to the euphotic zone (e.g., Knox, 1984; Sarmiento and Toggweiler, 1984; Kumar *et al.*, 1995; François, 1997). Regardless of the role of polar oceans in controlling atmospheric CO_2 levels on geological time scales, significant impacts of CO_2-mediated climate change on primary production and water-column grazing have already been reported in both Arctic and Antarctic waters, apparently driven by climatic effects on sea-ice dynamics (Smith and Sakshaug, 1990; Jacobs and Comiso, 1997; Smith *et al.*, 2001; Clarke and Harris, 2003). Further, benthic ecosystems, which derive much of their food from highly seasonal fluxes of primary production, are likely to be heavily impacted by any climate-induced changes in pelagic primary production (Smith *et al.*, 2005). However, the degree to which benthic ecosystems will be impacted by climate change will vary depending on the strength and time scales of the "benthic-pelagic coupling" between water column and seafloor processes.

High latitude ocean-atmosphere interactions have also been hypothesized to affect atmospheric CO_2 levels on much smaller scales. Yager *et al.* (1995) recently proposed the "seasonal rectification hypothesis", whereby summer phytoplankton blooms in an

Arctic polynya depleted total inorganic carbon levels in surface waters, creating a small sink in atmospheric CO_2 (Fig. 1). In low-latitude, ice-free waters, this carbon would normally have been returned to the atmosphere via respiration of bloom material. However, in seasonally ice-covered polar waters, this return to the atmosphere may be prevented by the formation of winter sea-ice, such that bloom-derived organic carbon is exported to sediments or offshore into deep water. While such hypothetical feedback loops are largely untested, they provide a useful framework for evaluating linkages between surface ocean and seafloor processes in seasonally ice-covered systems. Organic carbon appears to have accumulated to relatively high levels in Antarctic shelf sediments. However, climatic warming could enhance degradation of this material, while simultaneously altering sea ice coverage (and consequently, primary production), such that respired inorganic carbon would no longer be contained by seasonal ice coverage.

In addition to long-term trends in sea-ice dynamics and pelagic primary production, the Antarctic coastal environment experiences intense seasonal and interannual fluctuations in particulate flux to the seafloor, as evidenced by particle-trapping studies presented here (**Chapter 2**) and elsewhere (e.g., Wefer *et al.*, 1988; Dunbar *et al.*, 1989; Honjo, 1990; Smith *et al.*, 2005; Smith and DeMaster, in prep.). This short-term variability complicates observations of the effects of long-term, climate-induced changes in ecosystem function. Seasonal and multi-year, collaborative time-series sampling efforts like the FOODBANCS and Long Term Ecological Research (LTER) programs (cf., Baker *et al.*, 1996) are thus essential in removing some of the noise from decadal-scale trends. In addition, the dampening of seasonal and interannual variability in water column processes by sediments (**Chapter 2**; Smith *et al.*, 2005) suggests that benthic studies may be particularly useful in the tracking of long-term trends.

According to Smith *et al.* (2005), Antarctic benthic biomass correlates with water column productivity on regional scales, and is thus likely to be heavily impacted by climate-induced changes in primary productivity patterns. The relative ease with which benthic biomass measurements can be conducted and standardized may thus prove useful in long-term monitoring efforts. Further, benthos are said to act as "low-pass filters", integrating short-term oscillations in particle flux. Detritivorous benthos on the WAP shelf exhibited minimal temporal variability in feeding (**Chapter 3**; Purinton, 2005) or reproductive/recruitment patterns (**Chapter 4**; Galley, 2003; Glover *et al.*, 2005), further highlighting their ability to integrate short-term noise, and making them extremely useful as indicators of long-term ecosystem change in an environment with a high degree of temporal variability.

Conclusion and directions for future research

The paradigm of high temporal variability in Antarctic shelf ecosystems resulting from seasonal and interannual patterns in pelagic primary production has been brought into question by FOODBANCS results. Evidence of a persistent sediment "food bank" in deeper, soft-sediment habitats sets these areas apart from other, better-studied Antarctic benthic habitats such as the rocky near-shore areas. Temporal and spatial patterns in key benthic parameters such as community structure, sediment community respiration rates, and reproductive patterns must now be considered in a new light. Yet, while each of the preceding chapters furthers our understanding of the functioning of Antarctic benthic ecosystems, many additional questions are left unanswered, and still more have been presented by this work.

Assuming that other aspects of soft-sediment benthic ecology, like those presented here (feeding, recruitment), are intimately linked to the existence of the sediment "food bank", improved understanding of the factors involved in creating and maintaining this food bank is essential to the study of other benthic processes. The temperature-substrate hypothesis represents an important starting point for evaluating food bank dynamics, and must be rigorously tested if effects of warming on detritivore food availability are to be predicted. Sediment incubation experiments have been carried out in high-latitude areas in an effort to determine the effects of climatic warming on microbial enzymatic degradation of organic matter. However, these experiments have typically been conducted at saturating concentrations of substrate (e.g., Christian and Karl, 1995; Fabiano and Danovaro, 1998; Arnosti and Jørgensen, 2003; Bowman *et al.*, 2003; Mußmann *et al.*, 2003), which are suggested here to vary with temperature (Fig. 2.10). New experiments must be designed to test the *interaction* between temperature and substrate concentrations on enzymatic activity with natural Antarctic sediment microbial communities.

Understanding recruitment dynamics and the resulting patterns in abundance and community composition of macro- and megafauna (e.g., Glover *et al.*, 2005; Sumida *et al.*, 2005) depend on improved knowledge of the reproductive strategies in a greater number of Antarctic taxa. While a reasonable amount of data exists for certain megafaunal groups such as echinoderms (e.g., Pearse, 1994; Poulin and Feral, 1996), relatively little is known about the extremely diverse reproductive modes of infaunal polychaetes, which dominate soft-sediment macrofaunal communities on the WAP shelf. In addition, timing of larval release and length of time spent in the water column (and thus, degree of larval dependence on planktonic food sources) will shed light on questions of how reproductive patterns are, or are not, linked to seasonal bloom dynamics.

Additional tests of the role of a sediment food bank in benthic processes might include studies on growth-rate responses to seasonal phytodetritus flux. While broad generalizations have been made about extremely slow growth rates at low Antarctic temperatures (e.g., Clarke, 1988), seasonal increases in response to summer flux events have not been ruled out. Indeed, some well-studied taxa do show seasonally rapid growth and increased metabolism apparently linked to bloom cycles (Peck *et al.*, 1986; Peck *et al.*, 1987; Brey *et al.*, 1995; Brockington and Clarke, 2001; Brockington *et al.*, 2001; Brockington and Peck, 2001; Fraser *et al.*, 2002). Attempts were made during this dissertation research to determine relative changes in instantaneous growth rate using RNA:DNA ratios (cf., Bentle *et al.*, 1981; Dahlhoff and Menge, 1996; Buckley *et al.*, 1999). However, in attempting to improve upon published methodology, it was determined that uncertainties associated with the exclusive use of RNA:DNA ratios would make results difficult to interpret. The most desirable approach to this issue would combine measurements of a number of biochemical parameters (e.g., enzyme activities, uptake of labeled substrates in incubation experiments), and such approaches have recently been successful in Antarctica and elsewhere (e.g., Foster *et al.*, 1993; Fraser *et al.*, 2002).

In addition to an improved understanding of the basic biology for more benthic taxa, knowledge of temporal variability in environmental parameters on longer time scales (i.e., years to decades) is essential for identifying climate-related changes in Antarctic ecosystem health and functioning. Continued long-term monitoring programs such as the Palmer LTER program, as well as synthesis of existing data sets compiled around the continent over the previous decades, will broaden our ability to monitor the fate of this large and evolutionarily novel ecosystem.

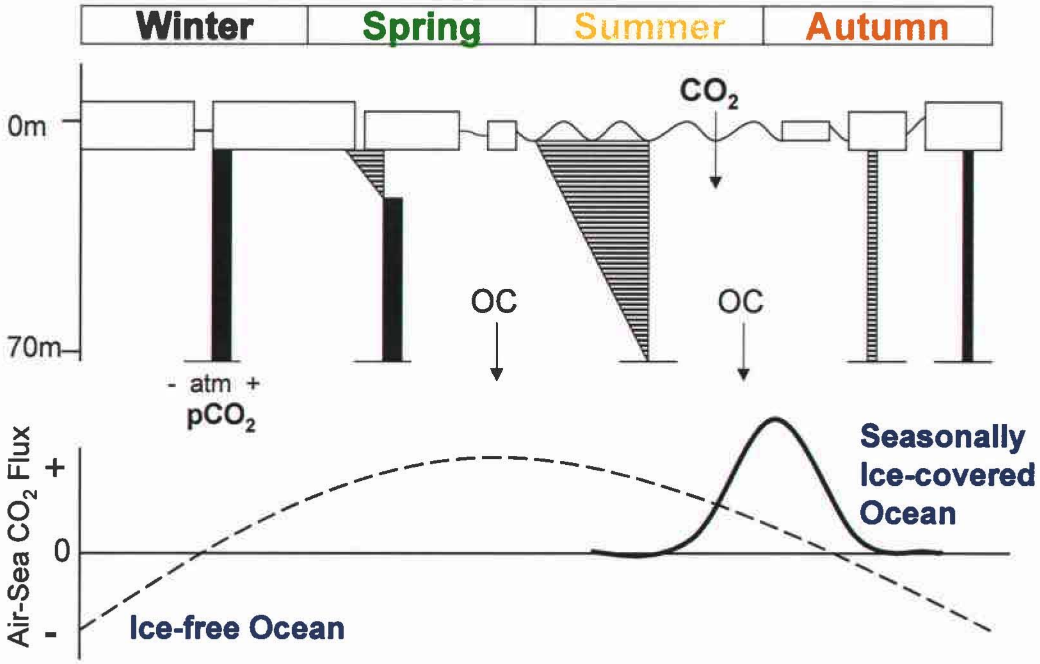

Fig. 1. Annual cycle of biological and physical processes affecting CO_2 cycling in seasonally ice-covered waters. Top panel represents vertical profiles of pCO_2 super- (solid) or undersaturation (striped) relative to the atmosphere, with ice-coverage represented by white boxes in surface waters. Bottom panel compares the typical seasonal air-sea CO_2 exchange in low-latitude, ice-free oceans and high-latitude, seasonally ice-covered oceans. (Redrawn from Yager *et al.*, 1995.)

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